Boris Kryštufek

Georgy I. Shenbrot

VOLES AND LEMMINGS

(Arvicolinae) of the Palaearctic Region

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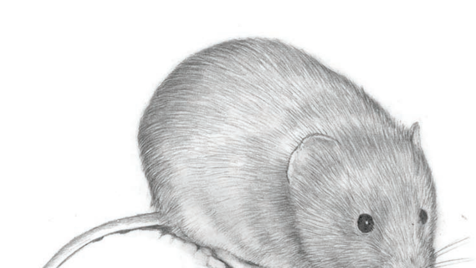

University of Maribor

Faculty of Natural Sciences
and Mathematics

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July 2022

Title **Voles and Lemmings (Arvicolinae) of the Palaearctic Region**

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Preface

Voles and lemmings (subfamily Arvicolinae) are the most specious and widely distributed rodents across the immense Palaearctic region, provided there is at least some available vegetation cover. They are keystone members and engineers of temperate, boreal and arctic ecosystems. Through their digging arvicolines aerate soil, increase groundwater recharge, and impact nutrient cycling, plant productivity and species composition. These effects are further emphasised through grazing which promotes ecological succession and creates habitats for other species. By transmitting ample amounts of cellulose and starch into proteins, arvicolines control the abundance of prey and predator species. Although small in size, they are large in the transfer of energy between the trophic levels.

As one would have thought, arvicolines are frequently used in various research endeavours of fundamental and applied significance, including research on small-mammal population dynamics, reconstruction of the impact of glacial-interglacial climatic dynamics on biodiversity and its survival in refugia, study of the evolution of metabolic rate and life-history strategies, and understanding the neuroscience of social behaviour. Arvicolines are of interest as reservoirs of infectious disease and as pests to agriculture and forestry. As they are ubiquitous in many fossil assemblages, their fossilised remnants provide accurate biochronological information and are widely used as a proxy of environmental change.

The majority of arvicolines are r-selected, have a short generation time and high population turnover rate. They furthermore show high rates of mutation change and chromosomal rearrangements, evolve promptly and abound with cryptic species. The number of recognised species nearly doubled in the last half-century and has still not stabilised. Experts engaged in medical zoology, epidemiology, biostratigraphy, zooarchaeology, population ecology, biodiversity conservation, museum collection management and many other biological subdisciplines who work on a daily basis with various arvicoline species are frequently baffled by the taxonomic changes and discordant classifications used in different sources. The aim of this review is to provide an up-to-date taxonomic review of the group within the Palaearctic borders. In particular we are attempting to ensure continuity between the earlier morphology-based taxonomies, karyology-based species delimitations and the current DNA-aided phylogenetic reconstructions.

This work provides a complete and independent list of Palaearctic voles and lemmings with descriptions, keys for identification, detailed distributional maps and basic taxonomic details allowing the user "to interpret intelligently and cautiously the results of taxonomists labour" (Corbet 1978:1). Although several recent compilations have addressed the topic, we still believe that the present work provides novel views. Truly, it is compilation but as we hope, a critical one, based on our first-hand experiences with various arvicoline species, assemblages and faunas throughout Europe and Asia gained during the last half century of our professional work. In 31 museums and collections across Europe, Asia and the USA, we examined well over 20,000 voucher specimens, including 302 name bearing types and 43 syntypes representing a further 13 nominal taxa. Of the 128 species recognised in this review, we saw all except 4. Maps were derived from an expanded earlier basis (Shenbrot & Krasnov 2005) which now contains 117,350 locality points. We studied literature on the topic, including original publications for nearly every taxonomic name published since 1758. And last, but not least, we discussed various issues of arvicoline taxonomy, zoogeography and biology with experts who actively study particular groups. We have received invaluable assistance from many experts and their comments and suggestions were most helpful, though, as usual, the opinions and mistakes remain our own responsibility.

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Taxonomy and nomenclature

Taxonomy is usually defined as the theory and practice of identifying, describing, and arranging (classifying) organisms into taxonomic groups on the basis of their relationships. A taxonomic system reflects, or should reflect the evolutionary history of the group under study, which in turn is imperfectly known. Systems are based on the existing scientific facts, other hypotheses and even intuition and are not the final truth. They are hypotheses of genuine evolutionary relationships and as such are subject to further testing, modification or rejection. Taxonomic systems are continuously changing as our understanding of phylogenetics advances.

An integral part of taxonomy is nomenclature, the arrangement of principles regarding creating and using scientific names to promote their stability and universality. The usage of a particular Linnean name is the consequence of the nomenclatural history of the name and regulations available through the International Code on Zoological Nomenclature (hereinafter referred to as the Code). Within arvicolines, one is confronted with names at three hierarchical ranks: the species group names (species and subspecies), the genus-group names (genera and subgenera), and the family-group names (the subfamily, tribes and subtribes). The nomenclature at each of these ranks was regulated by the 4th edition of the Code (ICZN 1999) to which we strictly adhere.

Authorities for taxonomic names with the year of publication are given for all Palaearctic taxa, regardless of their rank. Contrary to reference quotes in the text which have no comma between the author(s) name(s) and the year of publication (e.g. Ognev 1929), the name (or names) of a taxonomic authority (authorities) and the year are separated by a comma (e.g. *Alexandromys* Ognev, 1914). Type localities are provided for all valid species and subspecies. If quoted from the original source, the type locality is in quotation marks and any additional information is in square brackets. References to the original naming are provided for valid names, but not for their junior synonyms and invalid names. Type localities for all available names are shown on the species maps.

Family-group names

Prior to 1990, the name Microtinae Miller, 1896, was usually used for voles and lemmings (Figure 1) but has now been replaced by Arvicolinae Gray, 1821, which has absolute seniority. Some authors ranked the group as a family in its own right (Arvicolidae; Kretzoi 1955, Chaline et al. 1977, Honacki et al. 1982, Panteleyev 1998, Martin 2007).

In the late 19th century, Miller (1896) proposed a division of the subfamily into two supergeneric groups (Lemmi and Microti), and shortly afterwards Méhely (1914) advocated an alternative dichotomy into Fibrinae and Microtinae. Simpson (1945) proposed three such groups (Lemmini, Microtini and Ellobiini) while Musser & Carleton (2005) recognised ten tribes of which eight have Palaearctic representatives. Relying on recent phylogenetic reconstructions (particularly Steppan & Schenk 2017) we classify voles and lemmings into five tribes (see below). Main sources for the family-group names are McKenna & Bell (1997) and Musser & Carleton (2005). Family-group names are created from generic names by adding an extension: -idea (family), -inae (subfamily), -ini (tribe), and –ina (subtribe).

Genera and Species

In the Linnean taxonomy and nomenclature, the generic (genus) name is the first name of a binominal name (binomen). DNA-based phylogenetics brought much clarity into generic classification, however, molecular clusters which are ranked as distinct genera are not always definable morphologically. We have recognised 26 genera, which is a higher number compared to other revisions over the last century. Various authors writing on the topic after 1904 classified Palaearctic Arvicolinae in 14–23 genera (median=17; Figure 1). We frequently use a subgeneric rank which was avoided in some earlier reviews (e.g. Corbet 1978) but is gaining attention since the advent of molecular phylogenetics (Teta 2019).

Species is the central category in the majority of biological sub-disciplines. It therefore comes as a surprise that biologists frequently disagree on how to define a species and how to delimit two closely related species (de Queiroz 2007). In our pragmatic view, species are lineages which maintain their unique genetic makeups and occupy different niches. A hypothesis as to whether two sister lineages are conspecific or not can be tested in parts of their overlapping (sympatric) ranges. The confusion begins with the extension of the small-scale reality over space and evolutionary time, i.e. with the allochronic and allopatric populations. When in doubt, we compared data from the same marker between different pairs of sister species and extrapolated taxonomic inferences from better-studied cases. We have made every attempt to examine all the available information from different operational criteria. Further issues in species delimitation are posed by the limited hybridisation in overlapping (parapatric) parts of species' ranges. Documented cases of parapatric hybridisation are few in arvicolines, the zone of range overlap is usually narrow and the gene flow is frequently

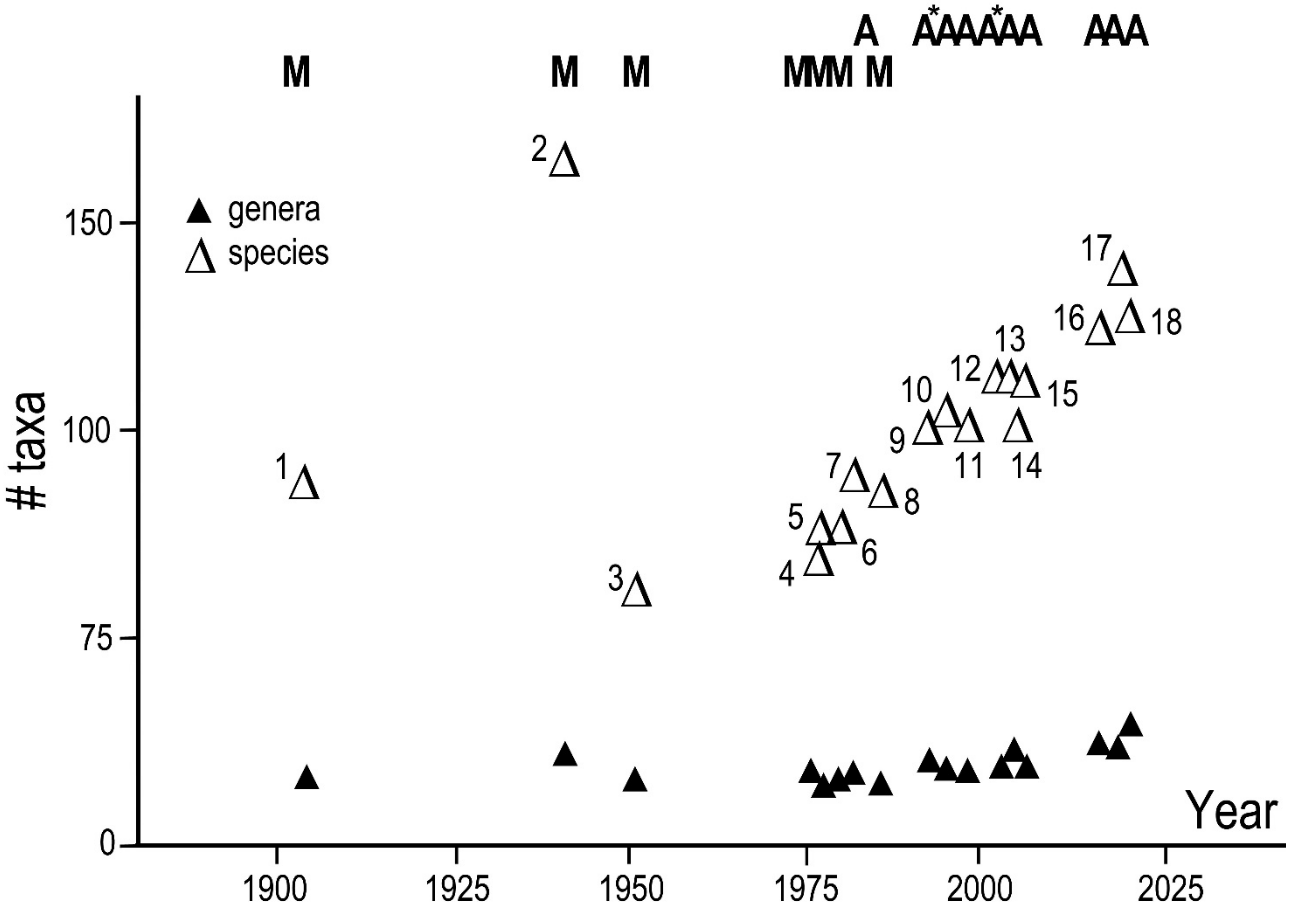

Figure 1: Number of species (△) and genera (▲) of voles and lemmings (subfamily Arvicolinae) recognised in the Palaearctic region by various authors since 1904. Bold upper case letters indicate the family-group name used by the authors: M – Microtinae, A – Arvicolinae (asterisk indicates a family rank Arvicolidae). Sources: 1–Trouessart (1904), 2–Ellerman (1941), 3–Ellerman & Morrison-Scott (1951), 4–Gromov & Polyakov (1977), 5–Corbet (1978), 6–Corbet & Hill (1980), 7–Honacki et al. (1982), 8–Corbet & Hill (1986), 9–Musser & Carleton (1993), 10–Pavlinov et al. (1995), 11–Panteleyev (1998), 12–Pavlinov (2003), 13–Musser & Carleton (2005), 14–Shenbrot & Krasnov (2005), 15–Pavlinov (2006), 16–Pardiñas et al. (2017), 17–Burgin et al. (2020), 18–this review.

restricted or nil. Most of our current knowledge on species diversity in Arvicolinae relies on morphological, chromosomal and mitochondrial (mt) DNA variation, and on cross-breeding trials. Phylogenetic reconstructions using nuclear DNA are sorely needed for testing the validity of recently recognised cryptic species.

At least 16 taxonomic lists of Palaearctic arvicolines have been published since Trouessart (1904) which recognised between 69 and 165 (median=100) species. The Nearctic muskrat *Ondatra zibethicus* which since 1905 has repeatedly been introduced from North America and is now widespread in Europe and boreal Asia (Pardiñas et al. 2017) is not considered. As evident from Figure 1, compilations were rare during the first half of the 20th century and the number of recognised species varied dramatically between sources. Ellerman & Morrison-Scott (1951), who strictly adhered to a polytypic species concept, recognised less species than any other review. Although they are frequently blamed for the "taxonomic inertia" which followed during the second half of the 20th century, their species list laid the groundwork for the steady taxonomic progress which has followed from the 1950s right up to now.

Main sources for the genus- and species-group names are Trouessart (1897, 1904, 1910), Palmer (1904), Miller (1912a), Allen (1940), Ellerman (1941), Ognev (1948, 1950), Ellerman & Morrison-Scott (1951), Corbet (1978), Pavlinov & Rossolimo (1987), Kretzoi & Kretzoi (2000), and Musser & Carleton (2005).

Subspecies

Since the late 19th century mammalogists have applied subspecies names to define infraspecific geographic variation. The practice gained popularity with the acceptance of the polytypic species concept but ever since the 1950s was subject to repeated attack. At present, the situation with trinomial taxonomy is ambiguous. Subspecies are rejected by many claiming that the rank is imaginary and, as such inefficient and superfluous for reference purposes. Opponents argue that the deficiencies attributed to the subspecies system are more a matter of excess and misuse in the application of the concept, rather than of the concept itself. In any case, subspecies remains in use as the lowest category recognised in formal taxonomy and is sanctioned by the International Code of Zoological Nomenclature.

As was common with mammals in general, subspecies in arvicolines were also erected on morphological evidence, frequently from a single population and diagnosed by a small number of traits. Variation was only exceptionally quantified and mapped to discern the pattern for subsequent classification. Various subspecific forms are based on slight differences with no proof of discontinuity (cf. the purported subspecific diagnoses in Niethammer & Krapp 1982, and Gromov & Erbajeva 1995). DNA-based phylogeographic assessments on the other hand repeatedly retrieved geographic structuring similar to the one stipulated by the advocates of a polytypic species concept evidencing that subspecies are potentially real and meaningful. Little has been done in Palaearctic arvicolines to link phylogeographic lineages with traditional subspecies in order to build robust subspecific taxonomies. In this review we did not entirely reject the subspecies but were still cautious in formalising subspecies.

Geographic setting

Voles and lemmings are a Holarctic group. Of the 161 species listed in Pardiñas et al. (2017), only four are Transberingian, while the remaining are exclusively Nearctic (38 species) or Palaearctic endemics (119 species). In the past, the Transberingian species were believed to be more numerous and at some stage the following species pairs were considered as conspecifics: *Microtus arvalis* (Palaearctic) – *M. montanus* (Ellerman 1941), *M. agrestis* – *M. pennsylvanicus, Stenocranius gregalis* – *Microtus miurus,* and *Clethrionomys glareolus* – *C. gapperi.* Arvicolines transgress the southern Holarctic border in both continents and several genera are predominantly or exclusively Oriental (*Hyperacrius, Caryomys, Eothenomys, Anteliomys*). Despite this, we covered the Euro-Asiatic arvicolines in their entirety. A single vole is endemic to the Palaearctic Africa.

Distributional ranges of 128 Palaearctic arvicolines cover surface areas between 334–17.5 million km^2, i.e. a difference of more than four orders of magnitude. Frequency distribution is heavily skewed towards small areas (mean=1,088,561 km^2, median=97,719 km^2) and half of all ranges measure 26,000–517,000 km^2.

Arvicolines are better at conserving heat than in dissipating it, hence they are poorly equipped to thermoregulate at high ambient temperatures. Unsurprisingly, throughout the Holarctic they are the

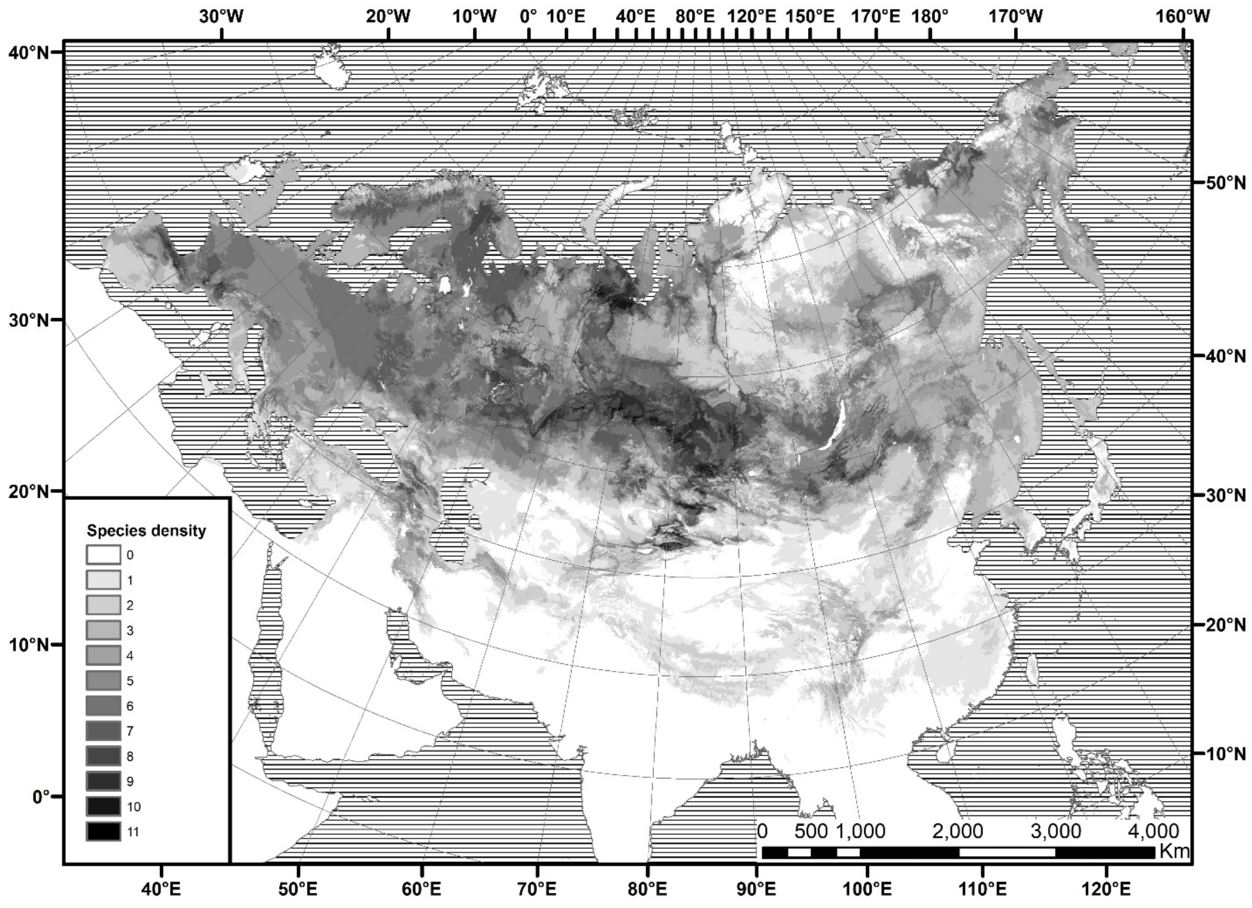

Figure 2: Species density of Palaearctic voles and lemmings. The darker the colour, the higher the number of species per unit area.

most abundant in terms of species and individuals in boreal and northern temperate regions. Few species occupy semideserts and the eastern Palaearctic true deserts; voles are however absent from deserts in the west (Figure 2). Along the southern distributional border, arvicolines search for shaded or wet (marshy) patches and frequently occupy high elevations. Along the elevational gradient they range from below sea level (–20 m) to 6,140 m, i.e. they ascend higher than any other rodent. One half of all ranges are at an altitude of 545–2,322 m.

Characteristics of Voles and Lemmings

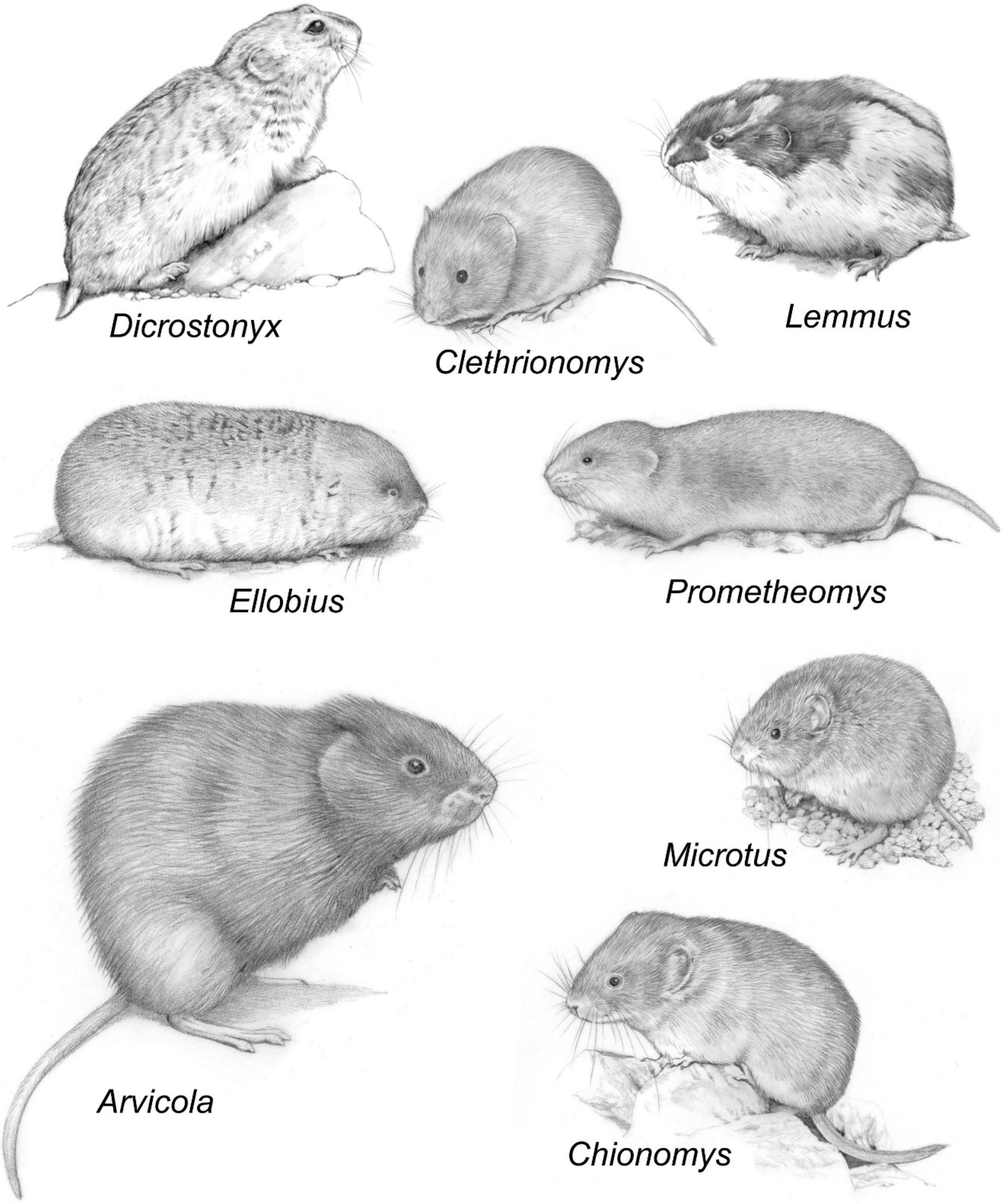

Figure 3: Representative genera of Palaearctic voles and lemmings. Art Jan Hošek. Used with permission of the Science and Research Centre Koper.

External appearance

The majority of arvicolines are of small size. Body form is robust and short-tailed. Tail is usually shorter than ½ of head and body and tapers towards the pointed tip; its cross section is circular. Head is large with a bluntly rounded muzzle; eyes are small. Limbs are powerful and although moderately long, they are hidden in the integument of the trunk, hence giving a short-legged appearance (Figure 3). Hind feet are plantigrade and usually longer than the digitigrade fore feet which in turn tend to be broader. The feet each have 5 digits but the thumb is always distinctly smaller and usually reduced to a mere vestige.

Skin derivatives

The rhinarium, a hairless and specialised skin surrounding the external openings of the nostrils (external nares), is of general murine type. The dorsal and ventral margins of nares are swollen forming the dorsum (above the nostrils), the infranarial region (below each nostril), the paired *alae nasi* (on the flanks of nostrils), and the internarial area (between nostrils); the internarial region is medially divided by a shallow sulcus (Figures 13c & 119). Some authors (Ognev 1948, Gromov & Polyakov 1977) denote the dorsum and the infranarial area as upper (superior) and lower (inferior) *allae nasi* (nasalis), respectively. Towards the upper lip, the infranarial area continues as the medial cleft (philtrum). Rhinarium is situated on the tip of the snout and comparatively high above the upper incisors but the distance is shorter in fossorial voles (Vinogradov 1926a, Brown 1972). The lips are furred and their lobes, along with the medio-ventral infoldings fill the oral cavity between the incisors and molars. The hypertrophied incisors are seen from the outside (cf. Figure 118h) however the entrance to the cavity is tightly closed by the labial lobes (Figure 4). The lobes are comparatively poorly developed in lemmings (Dicrostonychini and Lemmini) and in Clethrionomyini but come close together or even meet in *Prometheomys* and in the majority of Arvicolini. In Bramina the lobes fuse to each other across the mid-line (Vinogradov 1926a,b). The palate is covered by a mucous membrane which forms transverse ridges. Usually, there are 3 diastemal and 4–6 inter-molar ridges.

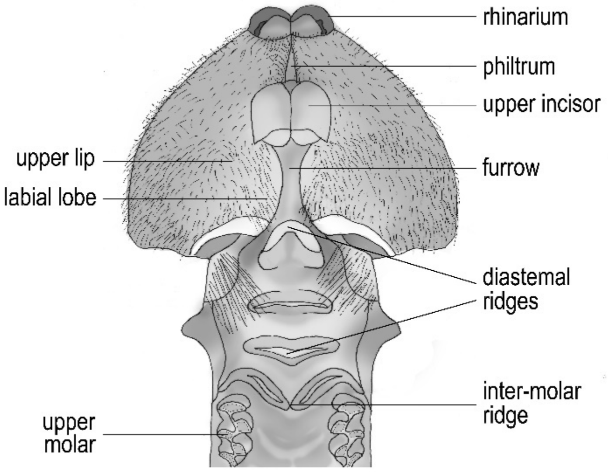

Figure 4: The diastemal palate in *Microtus arvalis* as viewed from below.

The auricle is typically small to moderately large, rounded and rather concealed in the fur. The lateral facies is usually structured with helicis, *plica principalis* (pinna), and antitragus; the prominence of the tragus varies (Figure 5). In *Dicrostonyx* and Bramina, the ear is reduced to a small projection around the meatus (Figure 118g).

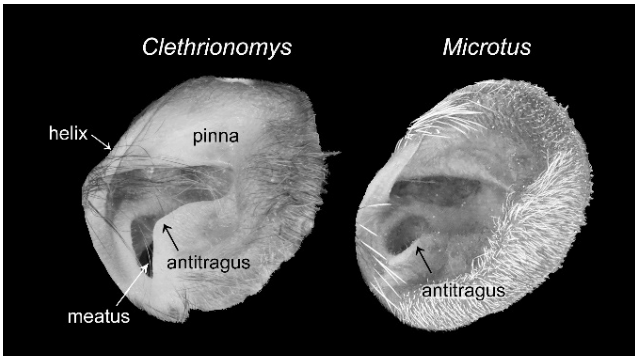

Figure 5: Left auricle in *Clethrionomys glareolus* (left) and *Microtus hartingi* (right). Not to scale.

Digits are equipped with curved and laterally compressed claws; the thumb has a small claw or its rudiment, a flat nail. The claws are narrower, longer and sharper in climbing voles (e.g. *Clethrionoyms, Chionomys, Dinaromys*) and broader, shorter and blunter in fossorial species. The front claws are frequently longer and may undergo various changes. They are much elongated in *Prometheomys* (Figure 14), and peculiarly modified in *Dicrostonyx* (Figure 19). The fore feet have 5 palmar pads in nearly all species; pads are reduced to 4 in *Myopus* and are effectively absent in *Dicrostonyx*, *Lemmus*, and

Eolagurus. Typically, there are 6 plantar pads on the hind feet (e.g. Figure 49) but the lateral metatarsal pad is frequently absent, hence giving a count of 5 pads (e.g. Figure 204). Number of pads frequently varies between 5 and 6 even within the same species although one or the other count strongly prevails. In species which have been studied more in detail, asymmetry was detected in the same individual with different counts of pads on the left and right soles (e.g. *Alexandromys*). *Lagurus* has only 4 small plantar pads (Figure 138a) and in *Dicrostonyx, Lemmus* and *Eolagurus* the vestiges of pads are entirely concealed under dense hairs (Figures 25a & 138b).

All voles are furred. The hair densely covers the entire body except the auricle, the nasal pad, the distal portion of limbs and the tail. The tail is covered with scaly annulations that are partly or fully concealed by stiff hairs; terminal hairs normally form a tuft (pencil) of variable length and density (Figures 28, 48 & 241). The fur is of a simple structure. It consists of dense and shorter underfur and of longer and stiffer contour (guard) hairs. Fossorial voles normally have a mole-like pelage of short and dense fur with guard hairs not much longer than the underfur. Guard hairs are coarse and protruding on the posterior back of aquatic voles. Hair bases are nearly invariably slate and the fur is generally a shade of brown with blackish, buff, rusty, or yellowish tints. Light or black tips of longer stiff hairs give a grizzled appearance which is characteristic for many species. Voles from humid habitats tend to be darker and those from arid regions are more buff. A high proportion of black individuals is typical of certain riparian populations of *Arvicola amphibius* and for fossorial voles. Voles occupying rocky environments (*Alticola, Dinaromys, Chionomys*) are frequently grey. Pelage is monochromatic and the belly is lighter and greyer than the back; clear demarcation along the flanks is rare. Some voles (*Lemmus, Dicrostonyx, Lagurus, Stenocranius*) have a black spinal (mid-dorsal) stripe. Subspecies of *Lemmus lemmus* display blotches of bright and dull fur (Figures 26a & 33), matching certain environments at certain times, e.g. birch woods in spring and subalpine tundra during autumn. The rich colouration can be aposematic (in combination with aggressive behaviour), protective (cryptic), or a mixture of both (Andersson 2015). *Dicrostonyx* and *Aschizomys* show seasonal polyphenism having white pelage during winter (Figures 24 & 81). Moult is of sublateral type, with replacement of hair starting ventro-laterally and progressing medio-ventrally and dorsally (Kryltzov 1964).

On the head are long and coarse tactile hairs, the whiskers (vibrissae). Mystacial vibrissae (*vibrissae mystaciales*) as the longest and most prominent are arranged in several rows on the snout. Further clusters of vibrissae are positioned around mouth and on the chin (Sokolov & Kulikov 1987). Whiskers are the longest in voles living among rocks and the shortest in fossorial species.

Voles and lemmings have sebaceous glands which are distributed all over the body and connect to hair follicles. Larger sebaceous glands are organised as pads situated on the cheeks (cheek gland) and in the posterior part of the body (postero-lateral glands). Position of the postero-lateral glands is group-characteristic and was used in taxonomy as far back as Miller (1896). These glands produce a waxy (oily) excretion and are frequently sparsely haired or entirely devoid of hair (Wallin 1967, Clarke & Frearson 1972). Postero-lateral glands can be present in one or both sexes (usually in old males) and are not seen at all times (Quay 1968). There can be a single gland (caudal and rump glands) situated in the sagittal plane, or two symmetrical and laterally placed glands (flank and hip glands; Figure 6a) (Quay 1968). The caudal gland is present in *Dicrostonyx*, the rump gland in *Lemmus* and *Myopus*, the hip glands in *Microtus* (reported in the subgenera *Microtus, Terricola*, and *Euarvicola*), *Alexandromys*, and *Lasiopodomys*, and the flank glands in *Clethrionomys, Alticola, Craseomys, Eothenomys, Eolagurs, Dinaromys, Arvicola, Neodon, Stenocranius*, and *Chionomys* (Quay 1968, Lehmann 1969, Claussen 1975). Posterolateral glands are absent in *Lagurus* (Kratochvíl 1962) and Bramina (Quay 1968).

Tarsal (Meibomian) glands are modified sebaceous glands situated in both eyelids of many mammals, including arvicolines. Although still imperfectly known, variation in their numbers associates with taxonomy. The combined number of tarsal glands in the upper and lower eyelids is high in Dicrostonychini (14–29), Lemmini (18–27), Clethrionomyini (6–25; usually >15) and Lagurina (21–26), but low in Arvicolina (3–11) and

Microtina (1–14; usually <10) (Quay 1954, Dearden 1959, Hrabě 1977, 1978, 1979).

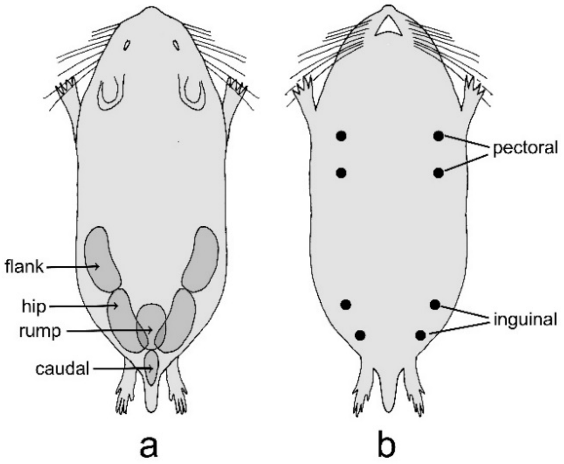

Figure 6: Schematic depiction of integumental structures in voles and lemmings: a–position of different types of the postero-lateral glands (nomenclature follows Quay 1968); b–a complete set of mammary glands.

Female Palaearctic voles and lemmings have 4, 6 or 8 nipples. Niethammer (1972) interpreted 8 nipples (2 inguinal and 2 pectoral pairs; Figure 6b) as the primitive condition in the subfamily. Eight nipples are present in all Palaearctic tribes; Clethrionomyini and Arvicolini also have 4 or 6 nipples. In such cases, both inguinal pairs are always present, except in Bramina. Bramina (6 nipples) are unique for retaining both pectoral pairs but losing an inguinal pair; an identical situation is known in the Nearctic *Microtus guatemalensis* and *M. ochrogaster* (Niethammer 1972). Liu et al. (2018) report 1 pectoral and 1 inguinal pair for *Eothenomys* (4 nipples) which contradicts Hinton (1923:147); this is typical of the Nearctic *Microtus mexicanus*. Further combinations of nipples were observed in Nearctic voles, along with up to 10 nipples in *Ondatra* (Niethammer 1972). Ognev (1950) reported 10 nipples for *Lasiopodomys* (as *Phaiomys*) but this is likely erroneous (cf. Allen 1940). Number of nipples can vary intraspecifically (e.g. in *Craseomys smithii* and some *Terricola*) and is rarely asymmetric in the same individual (cf. Meyer et al. 1996).

Penis and baculum

Voles have a simple barrel-shaped glans with a diameter accounting for 50–75% of the length (broader in *Ellobius*). A shallow terminal crater frequently has fingerlike processes. When not erect the penis is folded caudad and the glans is turned backward. Situated in the glans penis is a heterotopic bone called the baculum (*os penis* or *os priapi*). Its development is highly variable among species and its adaptive value is controversial. Because its morphology generally varies considerably between species but remains fairly constant within species, the baculum was frequently included in taxonomic studies. The arvicoline baculum is approximately 0.8–1.2-times as long as the glans and consists of a proximal shaft (proximal baculum, stalk) and a distal baculum (trident). The proximal baculum is dorsoventrally flattened and has an expanded base (Figures 62, 130, 159 & 265). The trident consists of three-pronged finger-like processes (digits) attached to the distal end of the proximal bone. The distal baculum can either be cartilaginous or osseous. Osseous processes consist of dorso-ventrally flattened medial process and two lateral processes which are joined by cartilage. Distal processes are ankylosed to the distal end of the shaft, either firmly or loosely. Shape of the baculum changes with age (Anderson 1960, Hooper & Hart 1962, Liu et al. 2017, Yato & Motokawa 2021).

Sperm head

Morphology of the sperm head proved useful in distinguishing sibling species of voles, hence we include this information when available. The head is one of the two component parts of the mammalian gamete (spermatozoon); the other one is the tail. The head is flattened and asymmetrical. It contains a nucleus (postacrosomal region sensu Fawcett 1975) with a haploid set of chromosomes. Overlying the nucleus is the acrosome (acrosomal cap or apical segment) of variable shape. Aksenova (1978) distinguished three main types of sperm head in arvicolines: (i) the acrosome is hook-shaped and caudally flexed (the head is falciform); (ii) the acrosome is conical and placed on the apex (the head is semi-oval); (iii) the acrosome is apical and submerged into the nucleus.

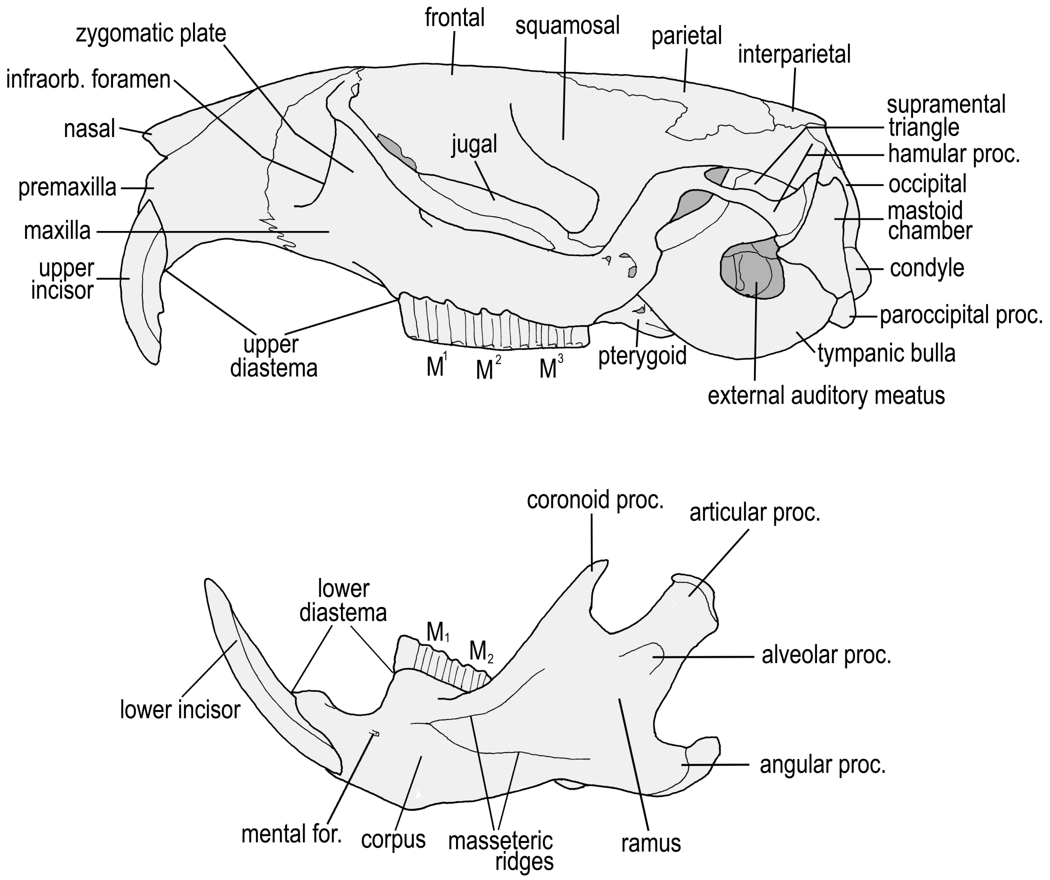

Figure 7: Lateral views of arvicoline skull (top) and mandible (bottom). Abbreviations: infraorb.–infraorbital; for.–foramen; M–molar; proc.–process; temp.–temporal.

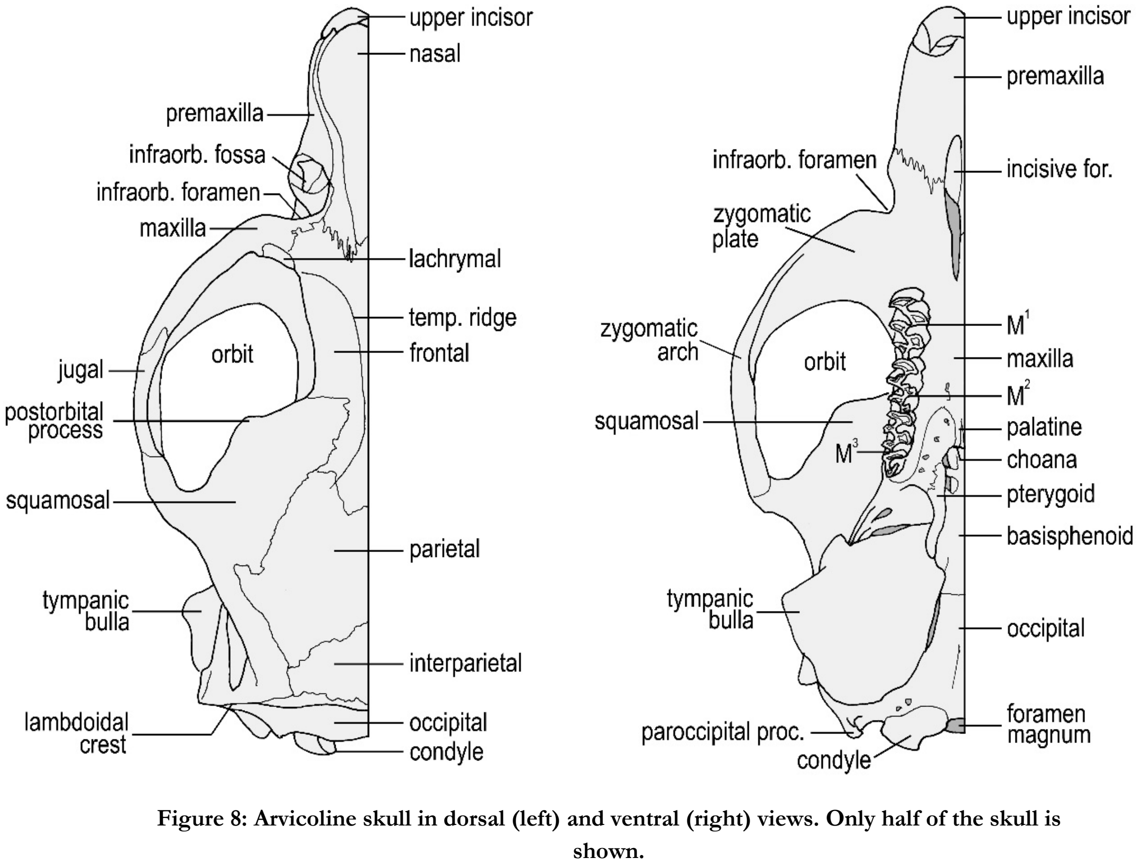

Figure 8: Arvicoline skull in dorsal (left) and ventral (right) views. Only half of the skull is shown.

Skull

Skull is massive with a short rostrum and straight dorsal profile (Figures 7,8). Nasals are short and do not usually overtop the anterior-most point of the rostrum. Masseteric (zygomatic) plate is broad, situated transversely or obliquely to the sagittal plane; infraorbital foramen is widened above for transmission of the enlarged medial masseter; its ventral portion is slit-like and obliterates in Bramina. Zygomatic arches are heavy and conspicuously broad in the jugal region. Zygomatic width usually accounts for 55–60% of the skull length and extreme shapes are rare. The skull is excessively narrowed in *Stenocranius* and widened in Bramina. The braincase, which is commonly rather deep, is flattened in some rock-dwelling voles, reaching the extreme in *Alticola strelzovi*. The interorbital region is narrow and the supratemporal ridges merge and form an interorbital crest in adults of some species. Anterolateral margin of squamosal bone has a prominent postorbital crest or process for attachment of anterior temporal muscle. Parietal and interparietal bones are typically large, but powerful temporal ridges may restrict them. The ridges usually diverge from behind the interorbital region and reach the maximal lateral expansion at the plane of glenoid fossa; posteriorly, they may converge, turning outwardly again at the level of the interparietal bone. The occipital region is either truncated or sharply sloped. Auditory bullae tend to be small in fossorial and amphibious voles and large in open-terrain species. The mastoid portion is sometimes inflated. The walls of the bullae are thin with no spongy tissues in Clethrionomyini, Pliomyina, and Hyperactina. In the majority of voles the walls of the bullae are spongy and the middle ear cavity is filled to varying degrees with ossified threads. Anterior palatal (incisive) foramina are moderately long (not reaching the level of M^1); in fossorial forms, foramina are frequently shortened and narrowed into a slit. A well-marked groove extends from the posterior end of each incisive foramen back to the maxillo-palatine suture or beyond, pass under the postero-lateral bridges and reach the postero-lateral pit (post-palatine foramen; *fossa palatina lateralis*).

The structure of the posterior palate demonstrates a significant taxonomic character. The two main palates can be distinguished (Figure 9), despite various intermediary stages (Hinton 1926a, Pozdnyakov 2008) (Figure 10). In the Clethrionomyini type, the palate terminates posteriorly as a simple shelf. The postero-lateral pits lie below (in fact, dorsal to) the palate level and open directly to choanae. The medial edges of pits usually do not communicate with the shelf and its medial spine ("nasal spine" of Hinton 1926a), when the latter is present. In the Arvicolini type, the medial spine extends posteriorly and merges with the medial edges of pits to form a sloping septum on each side of the mesopterygoid vacuity. The septum can be broad, short and ill-defined or long, narrow and prominent, or may assume an intermediate structure. Messopterygoid fossa extends between the last molars, while the postpalatine and parapterygoid fossae are absent in the majority of species.

The mandible consists of a horizontal corpus (horizontal ramus; *corpus mandibulae*) and vertical ramus (*ramus mandibulae*) with 3 processes: coronoid, articular, and angular processes (Figure 8). The articular process is usually set at an angle of 125–130^{o} against the horizontal ramus. Two prominent ridges on the labial surface of the mandible serve as attachments for major masseteric muscle and are consequently known as masseteric ridges (crests). They converge on the corpus at the level of M_1.

Dentition

All arvicolines have 1 incisor and 3 molars on both the left and right side of the upper and lower jaws (Figure 8), hence the total number of teeth is 16. The dentition is monophyodont. Incisors and molars are separated by diastema which in Palaearctic taxa is always longer than the molar row. Incisors grow from persistent pulps and have the front surface coated with enamel. This leaves the dentine naked behind, resulting in markedly unequal wear between the two surfaces which preserves a chisel point to the crown of the incisors. Typically, they are broad and smooth with a faint groove in some genera. The enamel on the front surface is usually stained yellow to orange. The upper incisors are proodont in several fossorial representatives but are orthodont in the majority of species. The upper incisors are strongly curved and pass backward into the maxillary to terminate in front of M^1. The alveolar sheath of the upper incisors extends further back in *Ellobius*, terminating on the hard palate mesial to molars. The lower incisors are longer and less curved. With respect to their length and position in the mandibular corpus, 2 main types can be distinguished. In the lemming type, the alveolar portion of the incisor is positioned lingually with respect to the molar row and terminates at the alveolar capsule below M_3. In the vole type, the incisor passes under M_2–M_3 from the lingual side to the labial side and ascends into the condylar process where it terminates in a well-marked bulge (*processus alveolaris*) (Hinton 1926a). This dissimilarity results from different timing in the development of the lower incisor and M_3. In the lemming type, the development of M_3 is accelerated and blocks the protrusion of the incisor towards the articular process. In the vole type, the growth of the incisor is advanced with respect to M_3, causing a lingual shift of the molar alveolus (Štěrba & Míšek 1982, Borodin 2014).

Molars are extremelly hypsodont, attaining arhizodont hypselodoncy (Renvoisé & Michon 2014) in most clades. They are mesiodistally long, angular and consist of multiple prismatic elements. The 1st molar is always the longest and the remaining molars are of approximately the same length. Length proportions in the great majority of arvicolines (M_2/M_1=0.70; M_3/M_1=0.26) differ from those in remaining Muroidea. (Renvoisé et al. 2009).

The pulp cavities remain open (arhizodont molars) for the whole lifespan in the majority extant clades except for *Prometheomys*, *Dinaromys*, Bramina, and some Clethrionomyina which retain rhizodont condition and develop roots with advanced age. Development of roots can be highly variable even within the species (see introduction to Clethrionomyini). Weekly rate of molar growth is 0.4–0.5 mm in *Lagurus lagurus*, 0.5–0.6 mm in *Alexandromys fortis*, 0.6–0.7 mm in *Lasiopodomys mandarinus*, 0.8–0.9 mm in *Dicrostonys torquatus* and 1.0–1.1 mm in *Alticola argentatus*. The entire molar crown is rebuilt between 6–12 months, depending on the group (Koenigswald & Golenishev 1979). The grinding surfaces are flat, composed of alternating dental triangles which are arranged in two parallel series and surrounded by transverse loops in which dentine fields extend across the tooth (Figure 11). Each lobe, cap or triangle is formed by dentine which is bounded externally by a sheet of enamel. The occlusal surface dentine shows shallow concavities representing sites of morphologically irregular dentine (reparative dentine) formed in response to irritations (Phillips & Oxberry 1972). The enamel-covered sides of the crown form a series of anticlines (salient angles) with the synclines (re-entrant folds, infoldings) lying in-between. Although lingual and buccal re-entrants are roughly equal in depth, the outer (labial) triangles are smaller than the inner (lingual) in many genera. Terminal angles on M^3 and M_1 are either acute or obtuse. In most voles, cement is present in the synclines. Triangles are classified as either opened (enamel of a re-entrant angle nearly or completely meets the opposing re-entrant angle) or closed (the two re-entrant angles are separate).

Upper molars consist of the anterior lobe (AL) and variable number of triangles (T). There are usually 4 triangles on the 1st upper molar (M^1) and 3 triangles on the 2nd upper molar (M^2). The 3rd upper molar (M^3) has a variable number of triangles and terminates with the posterior cap (PC; posterior prism or heel). The 1st lower molar (M_1) is the most complex and most frequently used in taxonomy. Its posterior part is a trigonid-talonid complex (TTC) which consists of the posterior lobe (PL) and 3 triangles. Except for few exceptions (*Prometheomys, Ellobius*), the TTC is invariant across the subfamily. The anteroconid complex (ACC) is positioned anterior to the TTC and carries the anterior cap (AC) and a variable number of triangles. The 2nd (M_2) and the 3rd (M_3) lower molars are of a simple structure, each consisting of a PL and four triangles which frequently merge into transverse loops. Outer triangles on M_3 are usually rudimentary (Meulen 1973, Semken & Wallace 2002). The most variable sections of dentition are the posterior part in M^3 and the anterior part of M_1. Molar pattern is conveniently used in taxonomy and distinct morphotypes may have diagnostic value. On the other hand, there is wide occurrence of homologous variability across species (Angermann 1974). Asymmetry is also common; e.g. in 10 species of Arvicolini, Kovaleva et al. (2019) found 27.7% of individuals with an asymmetric M_1.

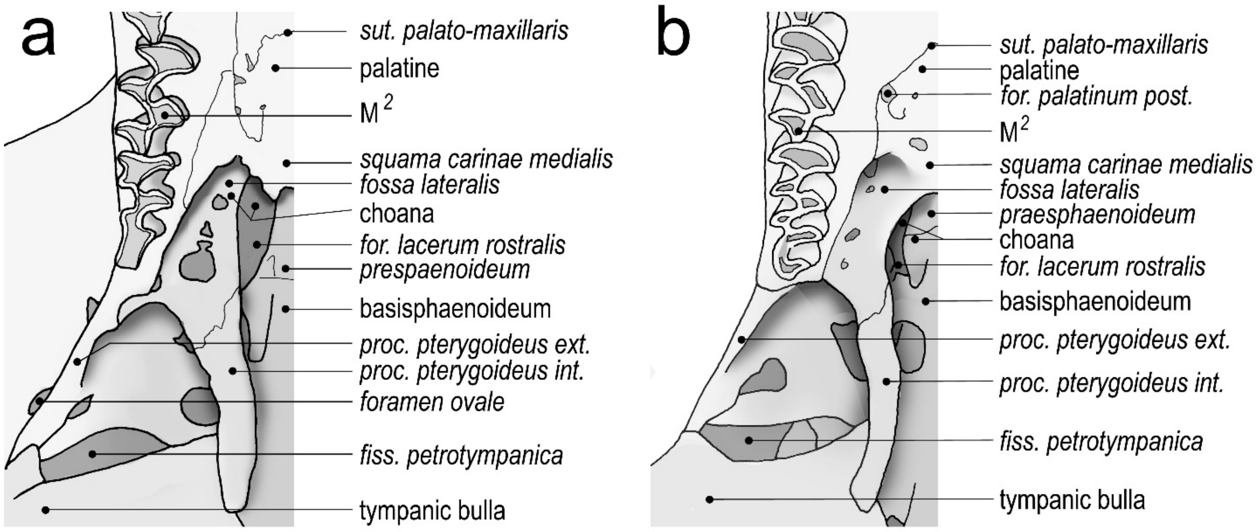

Figure 9: The main types of the palate in Arvicolinae rodents: a–Clethrionomyini type (*Alticola albicauda*); b–Arvicolini type (*Microtus montebelli*).

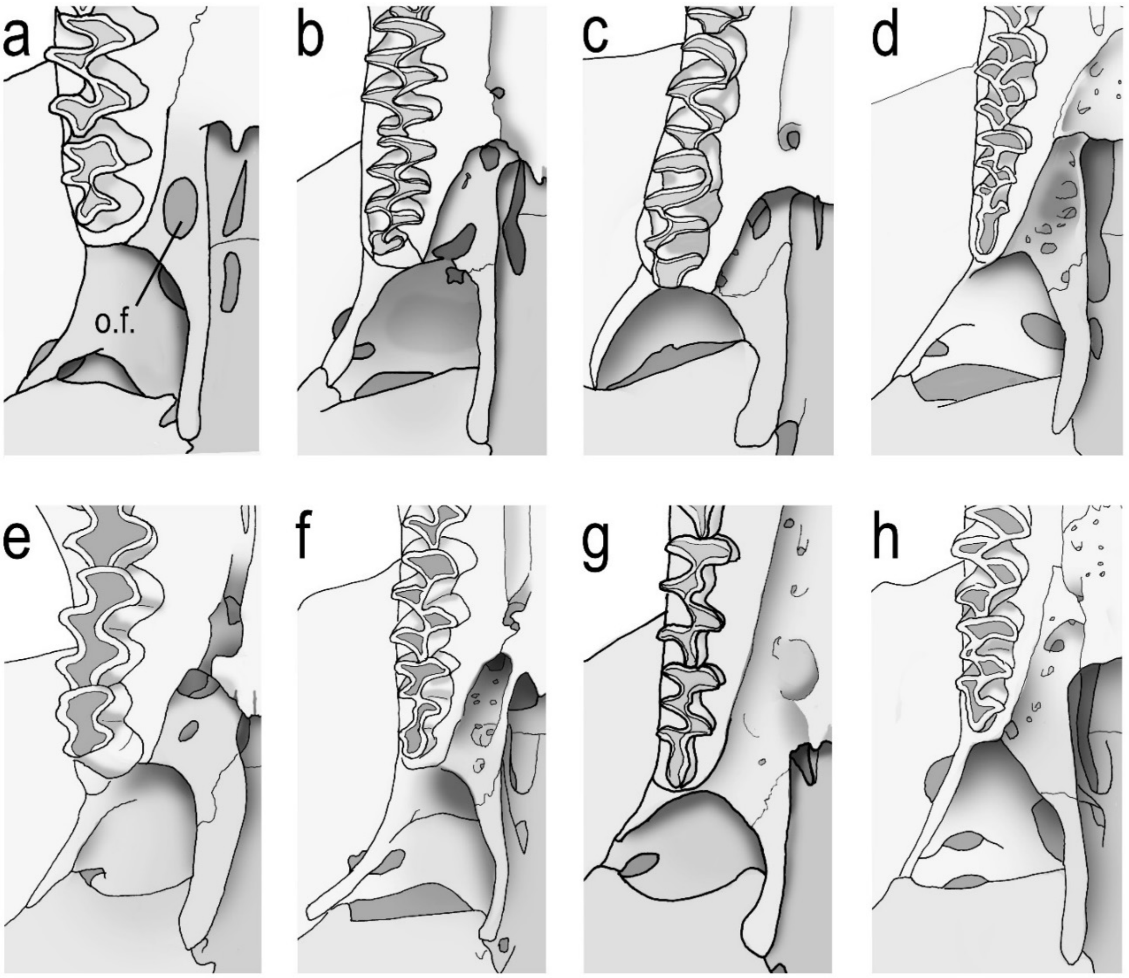

Figure 10: Posterior hard palate in main groups of Arvicolinae: a–*Prometheomys schaposchnikowi* (tribe Prometheomyini); b–*Dicrostonyx torquatus* (tribe Dicrostonychini); c–*Lemmus nigripes* (tribe Lemmini); d–*Caryomys inez* (Eothenomyina new subtribe, tribe Clethrionomyini); e–*Ellobius tancrei* (subtribe Bramina); f–*Hyperacrius wynnei* (Hyperacrina new subtribe); g–*Eolagurus luteus* (subtribe Lagurina); h–*Dinaromys bogdanovi* (subtribe Pliomyina). Subtribes e–h are classified into the tribe Arvicolini. Morphological structures are explained in Figure 9; o.f.–oval foramen.

The molars assume an adult pattern early in postnatal ontogenesis, e.g. in *Stenocranius gregalis* at the age of 1 month (Markova et al. 2013).

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The enamel layer that binds each tooth acts as a cutting edge during mastication. In primitive voles, the enamel is continuous, rather thick, and equally developed (undifferentiated) although the enamel becomes thicker in those portions exposed to higher abrasion during chewing. In arhizodont molars, the enamel plates are commonly thin or discontinuous at the apices of each salient angle. Because the two edges of the triangles assume different roles in mastication, they differentiate and vary in thickness in the majority of recent arvicolines. The convex edges (anterior edges of upper molars and posterior edges of lower molars) are defined as trailing (lee) edges, while the concave edges (anterior edges of lower molars and posterior edges of upper molars) are leading (luff) edges. Molars display negative differentiation when trailing edges are thicker than the leading edges and positive differentiation when the leading edges are thicker (Martin 2007).

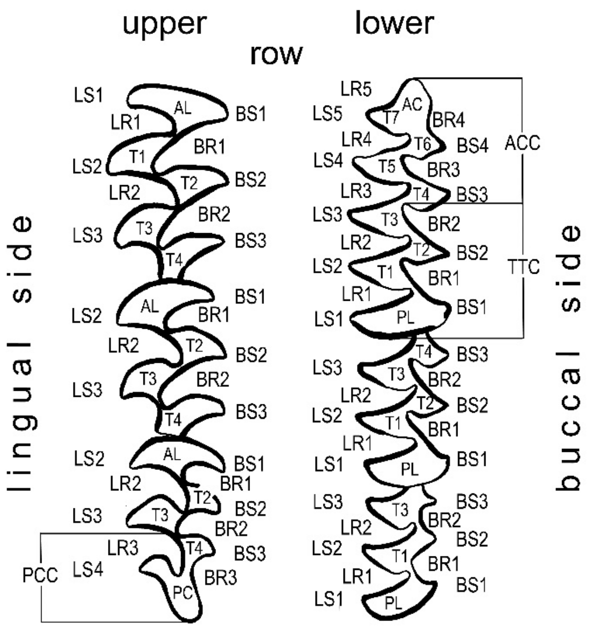

Figure 11: Dental nomenclature of arvicoline molars (after Meulen 1973). Occlusal surfaces are of left upper (maxillary) series (in *Chionomys*) and of right lower (mandibular) molar series (in *Dinaromys*). Lingual (inner) side is to the left and buccal (labial, outer) side is to the right. Anterior is to the top. AC–anterior cap; ACC–anteroconid complex; AL–anterior loop; BR–buccal re-entrant angle; BS–buccal salient angle; LR–lingual re-entrant angle; LS–lingual salient angle; PC–posterior cap (heel); PCC–posteroconid complex; PL–posterior lobe; T–dental triangle; TTC–trigonid-talonid complex.

The enamel consists of ~96% inorganic material (apatite prisms or crystals) and the rest is surrounding interprismatic matrix. Differences in the orientation of prisms (schmelztype) define the enamel banding pattern (schmelzmuster) which differs among major taxonomic groups. Three major types occur in arvicolines. The basic type is radial enamel with prisms rising against the outer surface of the tooth; the interprismatic substance takes orthogonal orientation against the prisms and is therefore oriented radially. Tangential enamel is typified by prisms and the interprismatic matrix running parallel to the occlusal surface. Lamellar enamel consists of bands (lamellae) that run parallel to the occlusal surface while the sequential layers are orthogonal. The interprismatic matrix strengthens the enamel in the third dimension. The radial type is presumably the most primitive and gave origin to the tangential type by turning the entire structure from 45^0 (primitive tangential enamel) to 90^0 (Koenigswald 1980, Koenigswald & Martin 1984).

Karyotype

Chromosomes are highly condensed parts of the genetic material and proteins which assume a threadlike structure during the metaphase of the cell division. Their number in a somatic cell is usually stable for a population and is reported as a diploid number (2n). Chromosomes of the same cell differ in size and shape. The shape is defined by the position of the centromere. When it is apical, the chromosome is acrocentric, otherwise it is bi-armed (meta- or submetacentric). The number of chromosomal arms (NF) gives a simple metrics of a conventionally stained set of chromosomes within the cell (karyotype). The name of chromosomes and their shape may vary within a single population or between them (polymorphism). Some polymorphic species show fixed differences between populations (polytypy) which usually originate from pericentric inversions or fusions/fissions of acrocentric/bi-armed elements.

Chromosomal evidence started to enter taxonomic research in the 1950s and resulted in considerable advances. By now, the vast majority of Palaearctic voles and lemmings have been karyotyped. Compared to other mammals the rate of chromosomal evolution is high in arvicolines in general and some lineages show a particularly accelerated tempo of change. This makes arvicoline rodents karyotypically one of the most polymorphic groups of mammals.

Abbreviations

External and cranial measurements:

BWt–body mass (weight);
HTL–total length (H&B+TL)
H&B–length of head and body;
TL–length of tail;
HF–length of hind foot;
EL–length of ear.
CbL–condylobasal length of skull (occipital condyle to the anterior-most point of the premaxillary);
OnL –occipitonasal length of skull (occipital condyle to the anterior-most point of the nasals);
ZgW–zygomatic width;
MxT–length of molar row.

Ratios (quotiens) are indicated by a slash (/); e.g. TL/H&B denotes a ratio of tail length against the length of head and body.

Molars are abbreviated by the upper case letter "M" with numbers 1–3 indicating their position in the row; superscript/subscript denotes upper (maxillary)/lower (mandibular) molars. E.g. M^2 is the 2nd upper molar. For further abbreviations of molar morphology see Figure 11.

Other abbreviations:

2n – diploid number of chromosomes
NF – fundamental number of chromosomal arms
NF_a – fundamental number of autosomal arms
mt – mitochondrial (genome, DNA)
Cyt*b* – cytochrome b
K2P – genetic distance calculated using the Kimura 2-parameter model
TMRCA – the most recent common ancestor
sp/spp. – species (singular/plural)
ssp/sspp. – subspecies (singular/plural)
ky/My (kya/Mya)–thousand/million years (ago)
a.s.l. – [elevation] above sea level
s. str. – sensu stricto (in a narrow sense)
$\bar{x}$ – arithmetic mean
SD – standard deviation
CI – confidence interval
~ approximately
≈ almost equal to
< / > less than / more than
≤ / ≥ less than or equal / more than or equal

SUBFAMILY:
ARVICOLINAE GRAY, 1821
VOLES AND LEMMINGS

The context of voles and lemmings within the classis Mammalia is as follows:

Class Mammalia Linnaeus, 1758
Subclass Theria Parker & Haswell, 1897
  Infraclass Eutheria Gill, 1872
    Magnorder Boreoeutheria Springer & de Jong, 2001
      Superorder Euarchantoglires Murphy, Eizirik, O'Brien et al., 2001
        Order Rodentia Bowdich, 1821
          Suborder Myomorpha Brandt, 1855
            Superfamily Muroidea Illiger, 1811
              Family Cricetidae Fischer, 1817
                Subfamily Arvicolinae Gray, 1821

Arvicolinae are in a sister position against true Palaearctic hamsters Cricetinae. Diversification of arvicolines started between 5.7±0.6 Mya (Conroy & Cook 1999) in Late Miocene (Fejfar et al. 2011) and 7.0 Mya (Steppan & Schenk 2017) and the group appeared in the fossil record some 5.5 Mya (Chaline et al. 1999). Modern classification and nomenclature of voles and lemmings is based on Miller (1896), Hinton (1926a) and Ellerman (1941).

Key to tribes and subtribes

1a) Lower incisors are short and positioned lingually with respect to molar row; they terminate below M_3 2

1b) Lower incisors pass under M_2-M_3 from the lingual side to the labial side and ascend into condylar process; they terminate posterior to M_3.... 3

2a) Pelage colour does not depend on the season; ears short but normally developed; front claws of normal size; skull is low with flat dorsal profile; re-entrant angles filled with cement; M_1 consists of TTC and AC (5 closed dental fields); M^{1-2} with 5 closed dental fields; triangles of M^3 form transverse laminas ....Lemmini

2b) Pelage is brown in summer, white in winter; ears are reduced to a low fold of integument; front claws of digits III and IV much larger during winter; skull is deep with evenly convex dorsal profile; re-entrant angles without cement; M_1 has 4 alternating triangles and AC anterior to TTC (9–10 closed dental fields); M^{1-2} with 7 closed dental fields; triangles of M^3 alternate ....Dicrostonychini

3a) Palms and soles are thickly hairy; lingual re-entrant angle LR2 of M^{2-3} with additional small salient angle ....Lagurina

3b) Palms and soles at least partly nude; lingual re-entrant angle LR2 of M^{2-3} without additional salient angle 4

4a) Molar pattern simplified; dental fields confluent; enamel band of molars is wide and not differentiated; re-entrant angles without cement 5

4b) Molar pattern not simplified; dental fields usually alternate; enamel band of molars is differentiated; re-entrant angles have cement 6

5a) Front claws grossly enlarged; 8 nipples; interparietal is remarkably small; pterygoid with oval foramen; upper incisors are orthodont ....Prometheomyini

5b) Front claws of normal size; 6 nipples; interparietal not reduced; pterygoid without oval foramen; upper incisors strongly proodont ....Bramina

6a) Palate terminates as a simple shelf; postero-lateral pits open directly to choanae ....Clethrionomyini

6b) Medial spine extends posteriorly and merges with the medial edges of pits to form a sloping septum on each side of the mesopterygoid vacuity 7

7a) Walls of auditory bullae without spongy tissue; M3: T2 is confluent with AL 8

7b) Walls of auditory bullae filled with spongy tissue; M3: T2 is separated from AL.........Arvicolina, Microtina*

8a) TL/H&B>0.55; mystacial vibrissae >50 mm; 6 plantar pads; re-entrant folds with cement; dental fields on M1–3 alternate ....Pliomyina

8b) TL/H&B<0.55; mystacial vibrissae <30 mm; 5 plantar pads; re-entrant folds lack cement; dental fields on M1–3 confluent ....Hyperacrina new subtribe

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* Arvicolina and Microtina differ in a combination of several traits. Arvicolina are large (CbL>30 mm) and have a simple M1 (T4 communicates with T5 and AC). Those Microtina, which are of large size, always have a more complex M1 (T4 isolated from T5 and AC); if T4 is confluent with T5 and optionally with AC, then size is smaller (CbL<30 mm).

TRIBE:

Prometheomyini Kretzoi, 1955

Prometheomyinae Kretzoi, 1955:355. Type genus is *Prometheomys* Satunin.

Taxonomy. An ancient lineage which may hold a basal position in Arvicolinae (Steppen & Schenk 2017). The tribe contains a single monospecific genus.

GENUS: *Prometheomys* Satunin, 1901 – Long-clawed Mole Voles

Prometheomys Satunin, 1901a:572. Type species is *Prometheomys schaposchnikowi* Satunin.

Prometheomys schaposchnikowi (Satunin, 1901) – Long-clawed Mole Vole

Prometheomys schaposchnikowi Satunin, 1901a:573. Type locality is "a [high mountain] Pass on the Georgian Military Road", and "not far from Kreuzberges [Krestoviy Pass above Gudaur] on the Georgian Military Road in the main chain of the Caucasus, ca. 6500' [1,980 m] high", Georgia.

Distribution (Figure 12). Endemic to the Caucasus. Distribution area of 58,566 km^2 is in 3 main fragments: (i) Western Caucasus in Krasnodar Krai, Adygeya, and likely also south-western Karachay-Cherkessia (Russian Federation) and Abkhazia; (ii) Central Caucasus in North Ossetia (Russia) and Georgia; and (iii) Lesser Caucasus in south-western Georgia and north-eastern Turkey. Main habitats are humid meadows with snow cover lasting for >200 days/year. Long-clawed mole-voles also occupy forest clearings, birch stands, orchards and arable land but avoid steep (inclination >25^0) slopes and rocky substrate (Vereshchagin 1959, Kryštufek & Vohralík 2005). Altitudinal range is 1,500–3,000 m a.s.l. with an outlier at 723 m.

Characteristics. A medium-sized fossorial vole which digs using enlarged front claws. Dimensions: BWt=52.5–101 g, H&B=125–169 mm, TL=36–57 mm, HF=20.8–25.0 mm, EL=10.5–14.2 mm, CbL=29.8–34.4 mm, ZgW=17.4–20.0 mm, MxT=7.0–8.7 mm. The eyes are small (diameter=2.1 mm) and the ears are conspicuous and sparsely covered by fur; they are rounded and equipped with barely detectable antitragus. Rhinarium shows no peculiarities; mystacial vibrissae are short and light (Figure 13). Feet have 5 toes each, equipped with long, slender claws; the claws are longer on the front feet (6.2–7.2 mm) than on the hind feet (<4 mm). Palms and soles are nude with 5 and 5–6 pads, respectively. Some pads (lateral metatarsal and palmar interdigital) may be reduced (Figure 14). Tail is moderately long (TL/H&B=0.27–0.43) and tapers gradually from a thick (~5.5 mm) base (Figure 15). Tail is densely haired and terminates into a pencil (length≈6 mm). Fur is up to 15 mm long, soft and moderately dense. Upper parts are dull grey-brown to cinnamon and the belly is greyish and shaded cinnamon; cheeks are usually buff. Hair bases are slate-grey and shade the ventral side. Juveniles are more greyish. Tail is uniformly brown with a white tip in ~½ of voles (51.4%, n=214). Feet and ears are dark brown. Females have 8 nipples.

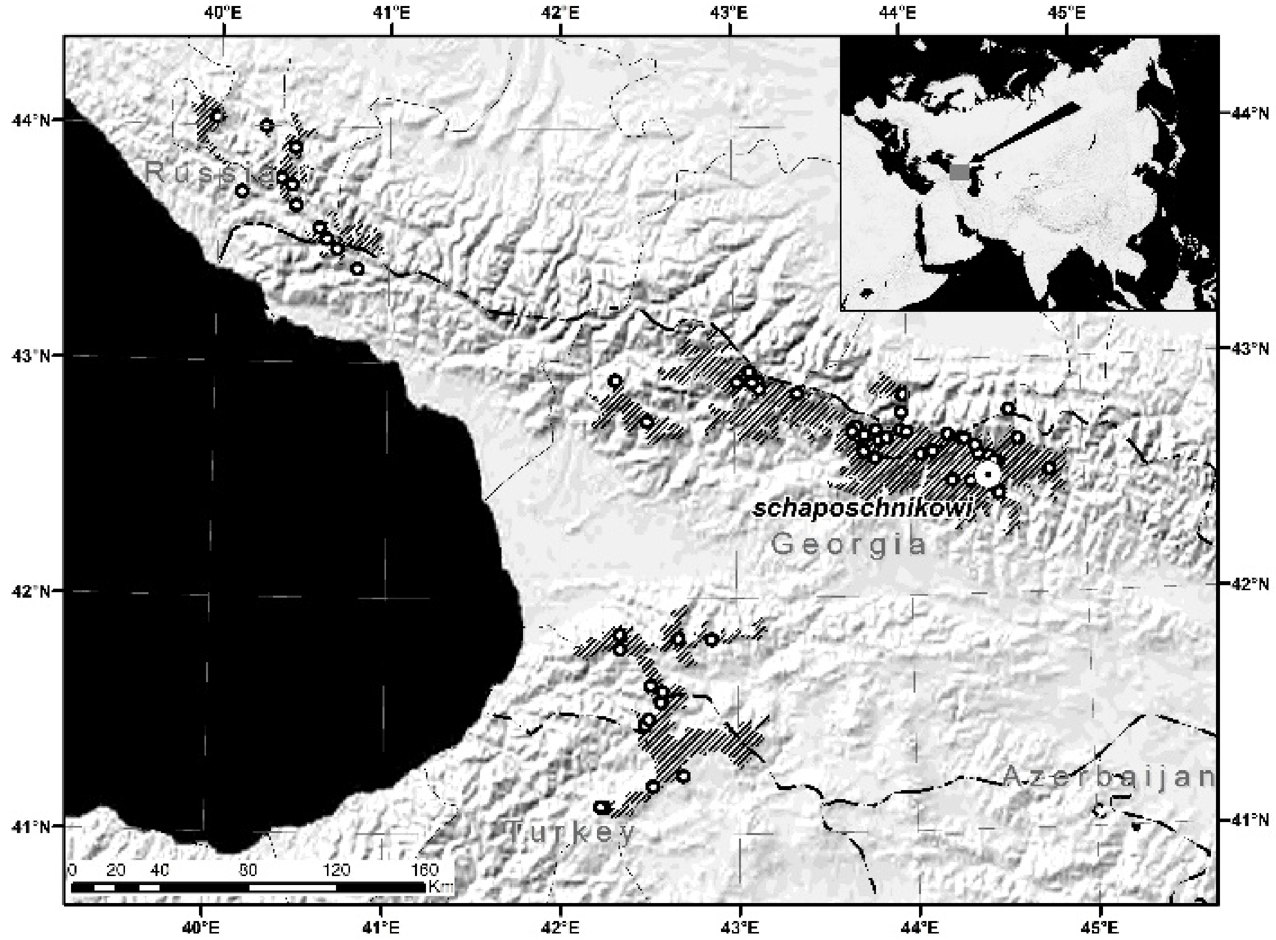


Figure 12: Distribution of long-clawed mole vole *Prometheomys schaposchnikowi*.

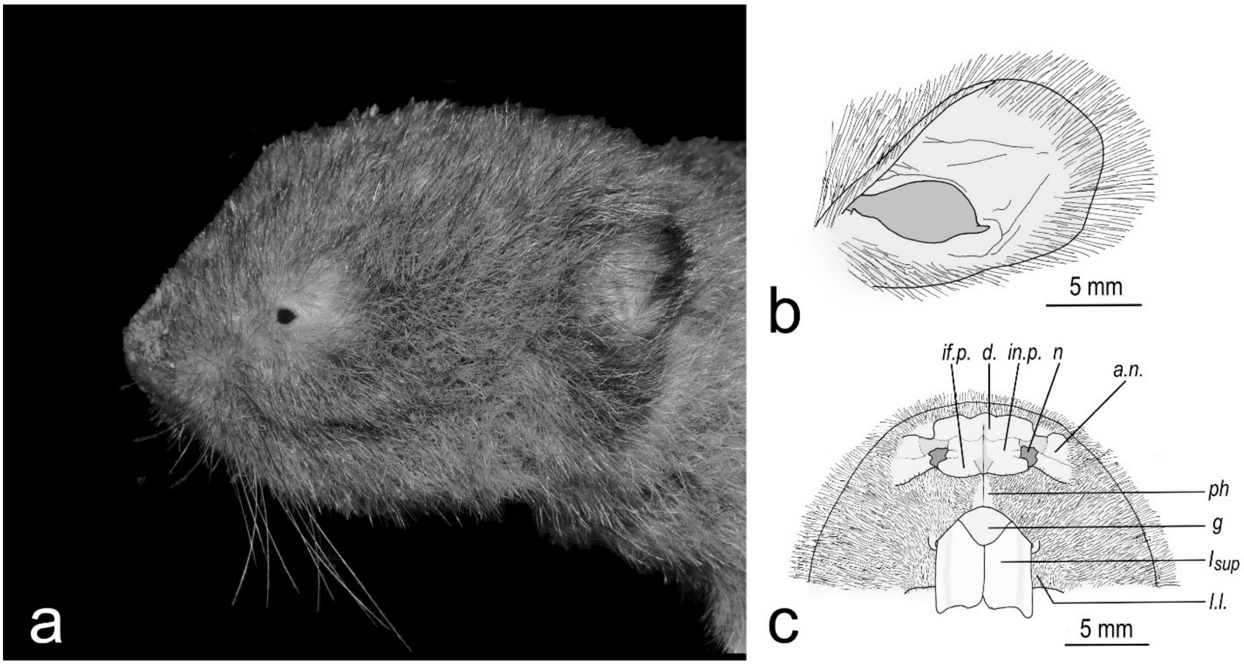


Figure 13: Head (a), ear (b) and the rhinarium (c) of *Prometheomys schaposchnikowi* from Gudauri, Central Caucasus. Note the small eye, relatively large ear, and short whiskers (inset a). Abbreviations in inset c: *Isup*–upper incisor; *a.n.*–ala nasi; *d*–dorsum; *g*–gum between the upper incisors *in.p.*–internarial portion; *if.p.*–infranarial portion; *l.l.*–labial lobe; *n*–nares (external nostrils); *ph*–philtrum.

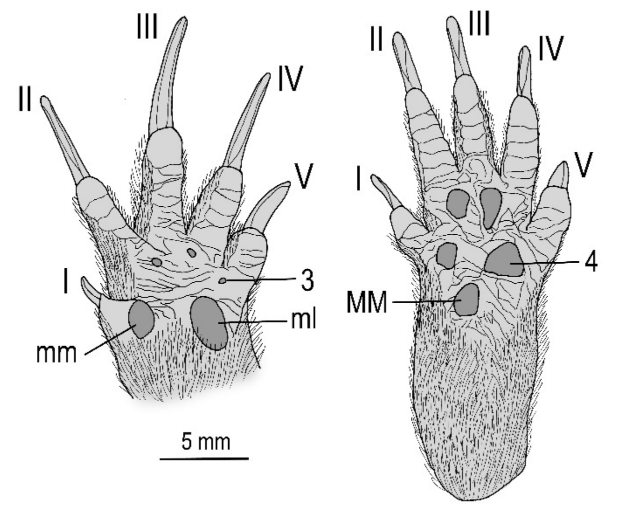


Figure: 14: Left palm (left) and sole (right) in *Prometheomys schaposchnikowi* from Gudauri, Greater Caucasus, Georgia.

Glans penis is simple and oval, 15.9 mm long and covered with spines. The baculum is composed of a proximal corpus (length=3.74 mm) and distal trident. Medial process (length=1.51 mm) is larger and more ossified than the lateral processes (Çolak et al. 1999).

The skull is robust with squarish brain-case, parallel zygomatic arches, and vertically truncated occiput (Figure 16). Rostrum is broad and moderately long, the interorbital constriction is well pronounced. Temporal ridges fuse into sagittal crest which extends from mid-interorbital region to the occiput. The sagittal suture from the nasals back to the interparietal bone does not obliterate but persists into advanced age; the interparietal is remarkably small and diminishes with age. Temporals are narrow but squamosals are very large. Incisive foramina are of moderate size. The posterior margin of the hard palate is unique in showing broad and complete postero-lateral bridges and shallow pits behind, each with a large oval foramen (Figure 10a). Medial spine is broad but does not merge with the medial edges of pits; hence there is no sloping septum on each side of the mesopterygoid vacuity. Bullae show no peculiarities and the *porus acusticus* is of normal size. The mandible has well-developed processes.

Upper incisors are orthodont with shallow longitudinal grooves. The root of the lower incisors passes onto the lingual side between the roots of M^2–M^3 and forms a bulge on the labial side of the articular process. Molars are rooted with 2 roots each; M^1 occasionally has 3 roots. In young voles, the alveolar capsules of the molars bulge in the floors of the orbit. Molar enamel is thick (0.14 mm), mainly of radial type but salient angles contain small amount of discrete lamellar enamel (Koenigswald 1980). The grinding pattern is simple with no sharp salient angles and dental fields of alternating triangles are frequently confluent; re-entrant folds lack cement (Figure 17). Anterior molars show all elements seen in other arvicolines. The anteroconid complex of M_1 consists of 2 triangles (T4–5) merging with the anterior loop. Posterior molars are the most reduced with only 2 lobes present in older individuals. M^3 is made of 2 loops and a single triangle (T2); a rudiment of T3 is visible in young voles. Unworn M_3 shows 2 re-entrant angles on each side but LR3 is obliterated with age.

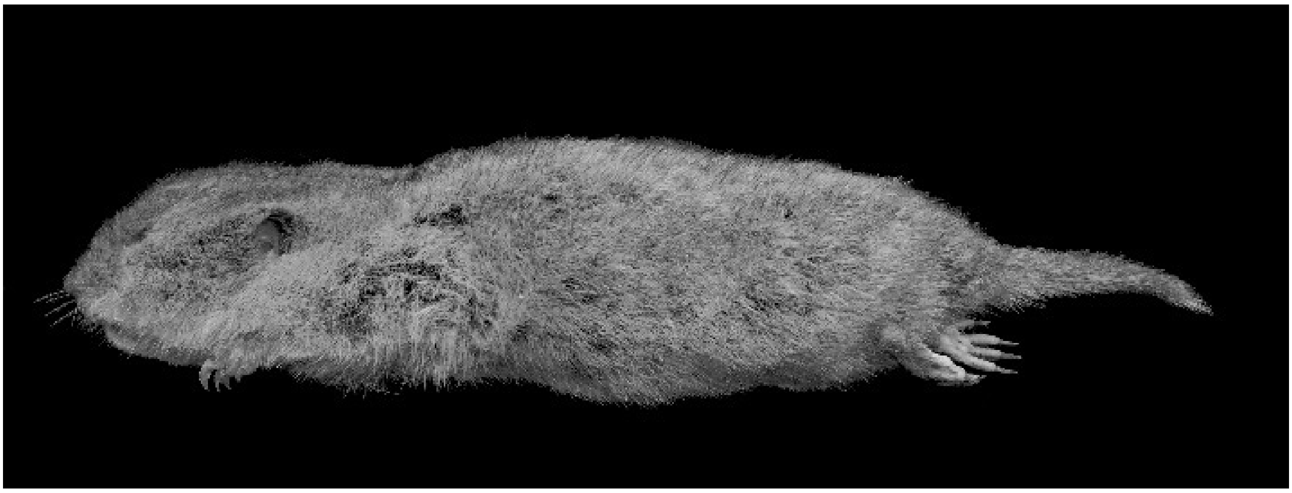


Figure: 15: Carcass of *Prometheomys schaposchnikowi* from Gudauri, Central Caucasus, Georgia. Photo F. Janžekovič.

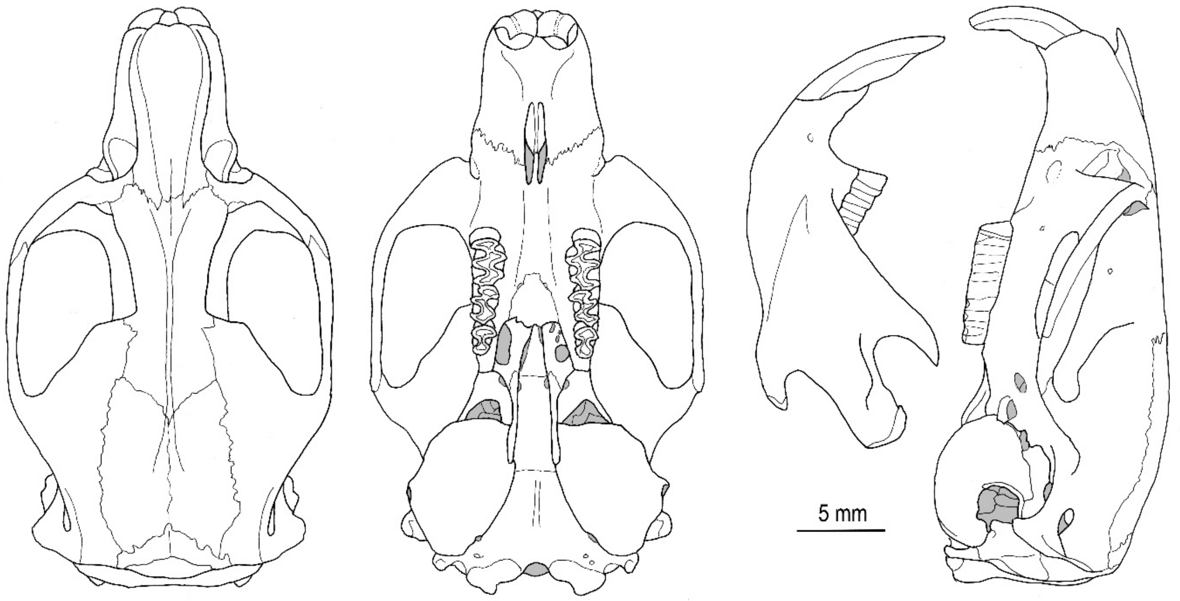


Figure 16: Skull in *Prometheomys schaposchnikowi* from northern Caucasus in Russia.

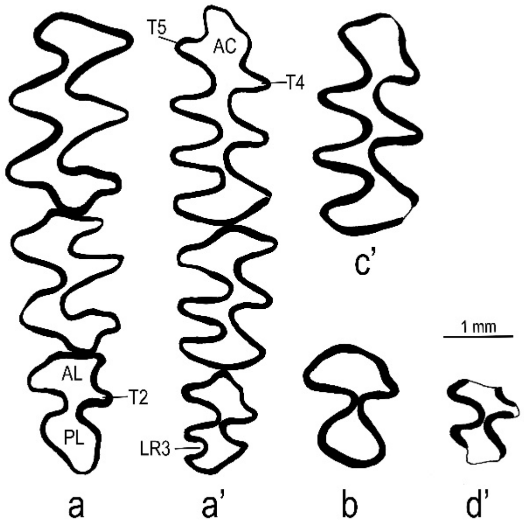


Figure 17: Molar pattern in *Prometheomys schaposchnikowi*: upper (a) and lower row (a’–Çam Geçidi near Ardahan, Turkey); isolated M^3 (b; northern Caucasus, Russian Federation); isolated M_1 (c’) and M_3 (d’–Gudauri, Georgia).

Karyotype (2N=56) consists of 11 bi-armed pairs while the remaining autosomes are acrocentric. All acrocentrics have short arms except for 4 pairs, which is the source of various opinions on the number of single- and bi-armed chromosomes. Two fundamental numbers are therefore reported: NF_a=70 (Zima & Kràl 1984) and NF_a=100 (Çolak et al. (1999). The Y chromosome is either metacentric or acrocentric.

Variation and subspecies. Monotypic species (Gromov & Erbajeva 1995). A melanistic population was reported from the western part of the range (Turov 1934); in the Upper Laba and Belaya Rivers, the proportion of black individuals is ~50% (Vereshchagin 1959).

TRIBE:
Dicrostonychini Kretzoi, 1955

Dicrostonychini Kretzoi, 1955:355. Type genus is *Dicrostonyx* Gloger.

Taxonomy. An ancient lineage originating from the first pulse of Arvicolinae radiation. The only Palaearctic representative is *Dicrostonyx*.

GENUS: *Dicrostonyx* Gloger, 1841 – Collared (Varying) Lemmings

Distribution. Circumpolar Arctic tundra, usually north of 55° northern latitude (Shenbrot & Krasnov 2005). The centre of species richness is North America with 6 extant species (Pardiñas et al. 1997).

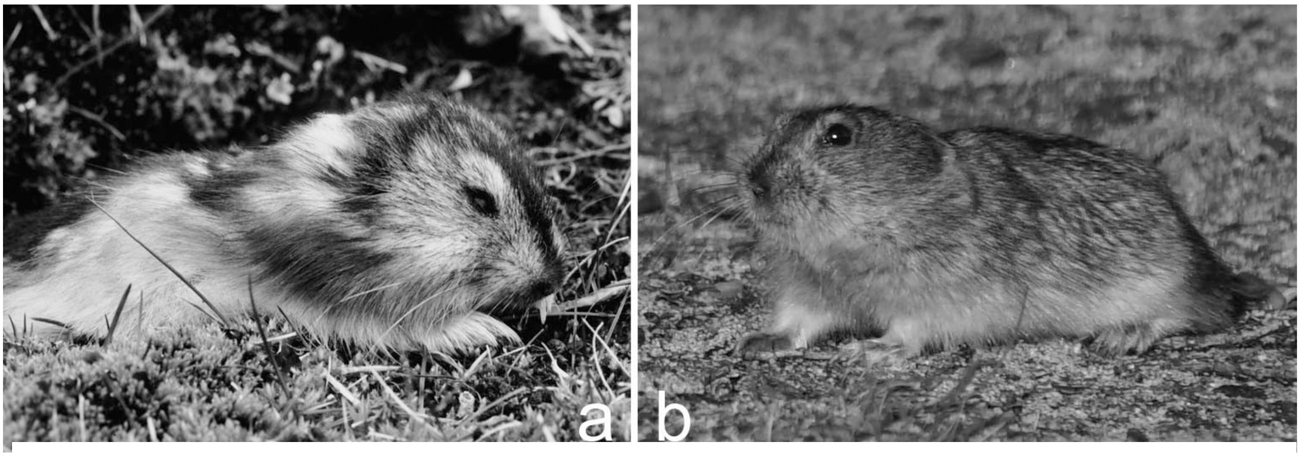


Figure 18: Collared lemmings with summer pelage: a– *Dicrostonyx torquatus* (Taymir, Russia); b–*D. groenlandicus* (Groenland). Photo courtesy: Gerard Müskens (a) and Sven Büchner (b).

Characteristics. Arvicoline rodents highly adapted to the extreme conditions of the Arctic tundra. Among others, they are unique in several seasonal adaptations as a response to the short photoperiod: whitening of pelage, increasing of size, modifying body shape to become rounder (Reynolds 1993), and developing large "winter claws" with bifurcate apex. Body is short and thick and the head is disproportionally large. Ears are reduced to a low fold of integument around the meatus; eyes are of moderate size (Figure 18). Tail is cylindrical, approximately the same length as the hind foot (TL/H&B=0.10–0.16), and the terminal pencil of bristle-like hair is as long as the tail itself (9–20 mm in *torquatus*). Hind foot is unusually large and strong; palms are short and exceptionally broad. Feet are densely furred on both sides; pads are entirely absent on palms and those on the soles are vestigial remnants at the base of the toes (Miller 1896). The thumb is barely perceptible with a tiny nail. Claws of manual digits III and IV are of normal size during summer (in *D. torquatus* the length of the claw on digit III is 6–10 mm; height ≤2.5 mm) but grow much larger in winter (length=11–15.5 mm, height 5–5.7 mm; Ognev 1948). The winter claw is the result of the fusion of the summer claw with the outward growth of the distal end of a toe pad which cornifies. The boundary between the two parts is denoted by a deepened lateral groove; differential wear during digging results in a notch at the groove between the dorsal summer claw and the hypertophied toe pad (Figure 19). Winter claws are partly lost during the spring moult and also worn down to normal-sized summer claws (Hansen, 1957). Summer fur in *D. torquatus* is 7–8.5 mm long on the belly and 10–11.5 mm on the mid-back; winter fur is softer and longer (9 mm and 12.5–17.5 mm on the ventral and the dorsal side, respectively). Summer pelage is greyish to brownish; cheeks are grey, front flanks and shoulders are rusty; belly is white to yellowish white with a broad buff or rusty collar on the throat. Winter pelage is white, rarely cinnamon-straw, pinkish or smoky grey, occasionally with blackish spots on the nose and between the eyes, or with buff patches on the shoulders and behind the ears. Some lemmings can be of intermediate colour (Dunaeva & Kucheruk 1941, Hansen 1959). Hair bases are slate regardless of the season and heavily cloud the colour of the fur. In *D. torquatus* the moult occurs in early April–May (white to brown pelage) and October (brown summer to white winter fur; Ognev 1948). Adult females have 8 nipples. Glans penis is highly distinctive due to the absence of dorsal papilla and the entire configuration of the baculum. The distal trident is cartilaginous or only partly ossified. The basal stalk is $\leq$3.1 mm long in Nearctic species (Anderson 1960, Ognev 1948).

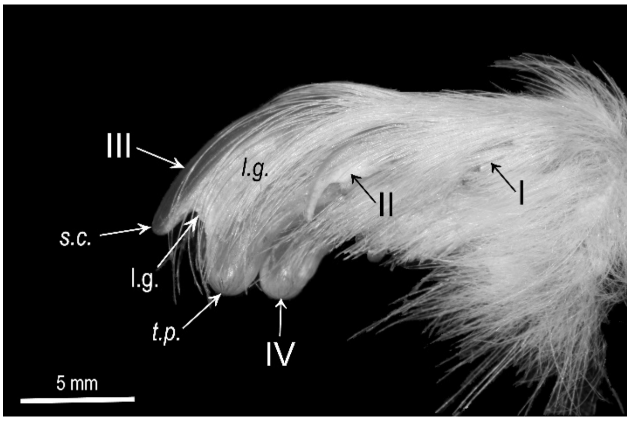


Figure 19: Right front foot in *Dicrostonyx torquatus* (from the Bolshezemelyskaya tundra, Russian Federation) with winter claws on toes III and IV. Abbreviations: *s.c,*–summer claw; *l.g.*–lateral groove; *t.p.*–cornified outward growth of the distal end of a toe pad; I, II–1st (thumb) and 2nd toes, respectively. Photo: B. Kryštufek.

Skull is lightly built but deep (depth behind M^3/CbL=0.35–0.42) and broad with widely expanded zygomatic arches (ZgW/CbL=0.64–0.67); profile is evenly convex. Rostrum and nasals are rather narrow and long, masseteric plate is high. Interorbital region is constricted and supraorbital ridges remain separated by a groove. Each squamosal develops a conspicuous peg-like postorbital process. Braincase is approximately as wide as it is long, while the interparietal is longer than it is wide. Incisive foramina are narrow and long but do not reach the level of M^1. Posterior edge of hard palate is essentially like in Clethrionomyini. The shelf terminates in a short median spine and incompletely covers post-palatal pits (Figure 10b). Interpterygoid vacuity is broad. Bullae are of modest size and the mastoid portion is somewhat inflated. The walls of the bullae are spongy; spongy bone also partly fills the cavity of the middle ear (Hooper & Hart 1962). Mandible is slender and coronoid process is short and blunt (Figure 20).

Lower incisor is of lemming type, i.e. short and with lingual position of its alveolar portion relative to molar row. Molars are rootless and lack cement in re-entrant folds. Enamel is positively differentiated with leading edge thicker than the trailing one; schmelzmuster consists of lamellar and radial elements (Koenigswald 1980). The enamel band is interrupted by dentine tracks at the vertices of all salient angles on all molars (Borodin 2014). Folding pattern is complex (Figure 21). M^1 and M^2 have 6 and 5 closed triangles posterior to the anterior loop, respectively; posterior triangles T6 and T7 are invariably small. M^3 has 3 re-entrant folds on each side and a short posterior lobe. M_1 is longer than M_2+M_3 combined in the lower jaw with 5 lingual and 4 labial deep re-entrant angles; anterior cap is confluent with triangles T8–T9. Posteriorly, M_2 and M_3 each have 4 closed triangles between the posterior lobe and the anterior vestigial loops T5–T6. Molars gradually became more complex throughout the Holarctic over the last 35 ka (Smirnov & Fedorov 2003). However, some modern populations retained the simple archaic pattern (Agadjanyan 1976). The archaic type lacks postero-lingual loop T7 on M^1–M^2, and antero-labial T6 on M_1 (Figure 21a–b').

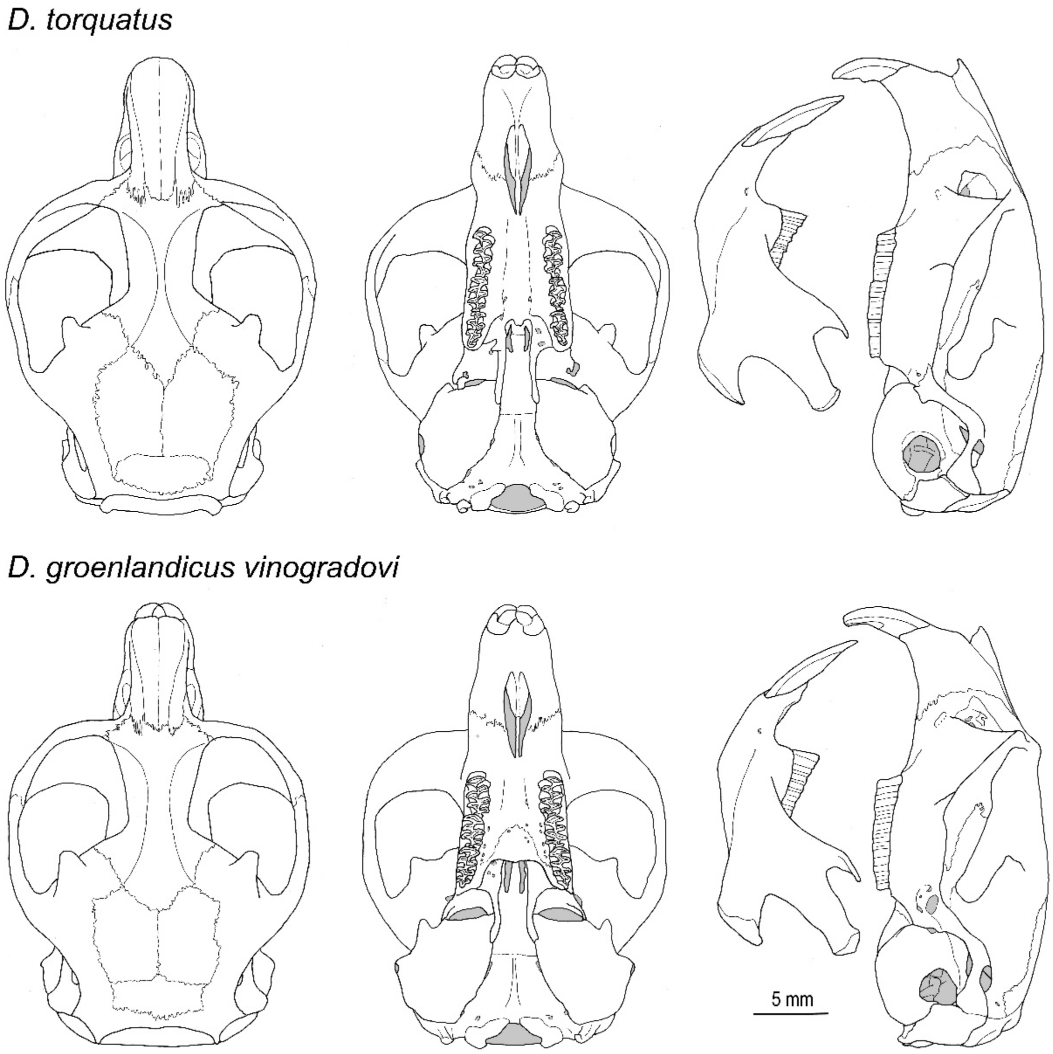


Figure 20: Skull and mandible in collared lemmings: top–*Dicrostonyx torquatus* (from Taimyrski Zapovednik, Krasnoyarsk Krai, Russian Federation); bottom–*D. groenlandicus vinogradovi* from Wrangel Island, Chukotka Autonomous Okrug, Russian Federation.

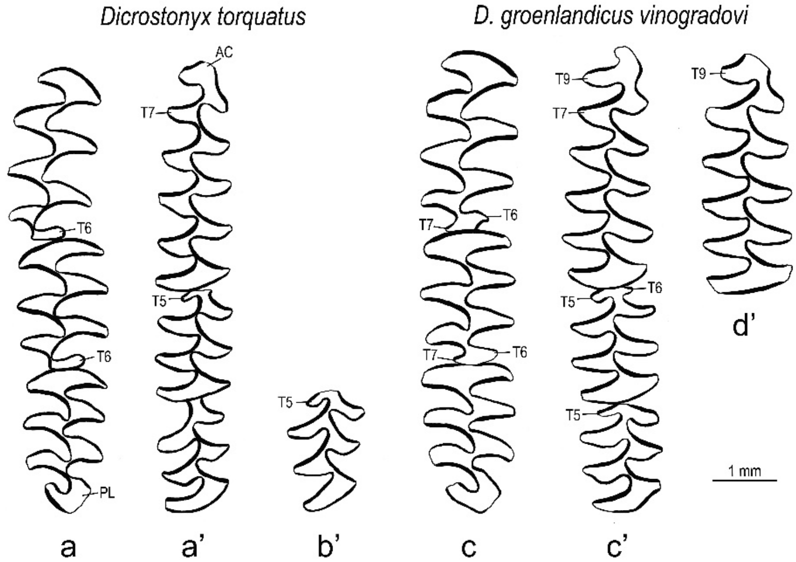


Figure 21: Occlusal molar pattern in collared lemmings. *Dicrostonyx torquatus* from Taimyrski Zapovednik, Krasnoyarsk Krai, Russian Federation: upper (a) and lower row (a'); isolated M_3 (b'). *D. groenlandicus vinogradovi* from Wrangel Island, Chukotka Autonomous Okrug, Russian Federation: upper (c) and lower row (c'); isolated M_1 (d').

Despite the distinctive grinding structure, the molar proportions in *Dicrostonyx* resemble the pattern seen in the majority of arvicolines, except for Lemmini which have relatively longer M_2 and M_3 (Renvoisé et al. 2009).

Key to species

1a) Karyotype 2n=37–48 (supernumerary B chromosomes usually numerous) …………….*torquatus*
1b) Karyotype 2n=28 (supernumerary B chromosomes never present)…………………..*groenlandicus vinogradovi*

SUBGENUS: *Dicrostonyx* Gloger, 1841

Dicrostŏnyx Gloger, 1841:97. Type species by subsequent designation is “an American species, probably *Mus hudsonius* Pallas” (Miller 1896:38).

Dicrostonyx groenlandicus (Traill, 1823) – Nearctic Collared Lemming

Mus Grœnlandicus Traill, 1823 (in: Scoresby 1823:390).
Type locality: “Jameson’s Land”, Greenland.
For Nearctic synonyms see Hall (1981).

Taxonomy. Collared lemmings from Wrangel Island were described as a subspecies (*vinogradovi*) of *torquatus* (Ognev 1948) but began to be treated as a species in its own right on the basis of karyological evidence (Kozlovsky 1974) and cross-breeding trials (Kuznetzova & Novokshanova 1988). Molecular analysis by Fedorov et al. (1999) provided further evidence for classification of *vinogradovi* in *groenlandicus*.

Distribution (Figure 22). Range (=3,343,830 km^2) extends from Alaska to Hudson Bay, encompassing the high arctic islands of northern Canada; also northern

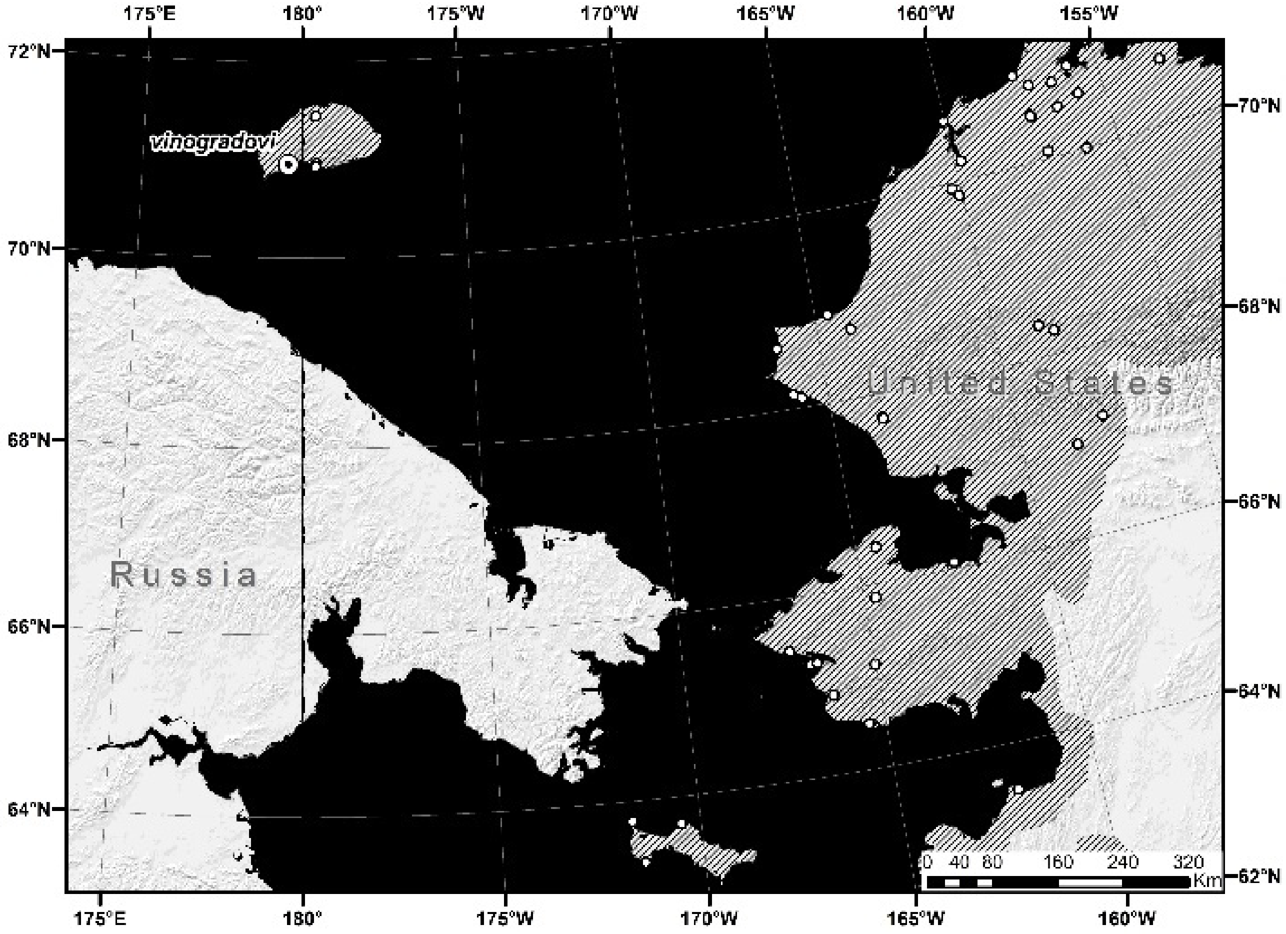


Figure 22: Distribution of the Nearctic collared lemming *Dicrostonyx groenlandicus*. Note that the only Palaearctic population is confined to Wrangel Island in the Arctic Ocean offshore Chukotka Autonomous Okrug of the Russian Federation.

and north-eastern coast of Greenland. Present on several Aleutian Islands and on the Bering Sea islands (MacDonald & Cook 2009). Altitudinal range is 0–1,800 m.

Characteristics. See under *vinogradovi*.

Variation and Subspecies. In addition to the Palaearctic *vinogradovi*, between 5 (Pardiñas et al. 2017) and 11 subspecies (Hall 1981) are recognised in the Nearctic part of the range.

Dicrostonyx groenlandicus vinogradovi Ognev, 1948 – Vinogradov's Collard Lemming

Dicrostonyx torquatus vinogradovi Ognev, 1948:509. Type locality: "Wrangel Island", Arctic Ocean, East-Siberian Sea, Far Eastern District, Chukotka Autonomous Okrug, Russian Federation.

Distribution. Endemic to Wrangel Island (Figure 22). The island is a distance of 140 km from the closest point on the Siberian mainland and has a surface area of 7,600 km². Lemmings occupy dry and upland tundra on slopes and riverine and coastal terraces up to 400–500 m a.s.l. (Chernyavskiy 1984).

Characteristics. Slightly larger but otherwise similar to *torquatus*. Dimensions: BWt=52–114 g, H&B=113–151 mm, TL=11–22 mm, HF=15.0–18.6 mm, CbL=28.0–32.7 mm, ZgW=18.3–21.0 mm, MxT=7.0–8.8 mm. Back is ash grey to grey-brown with a variable extent of buff or dull rusty wash; admixture of hairs with grey, black dull rusty tips gives a speckled appearance. Shoulders and front flanks are rusty to chestnut brown. The rump and head usually remain grey; fur is reddish around pinnae. Belly is whitish or light-grey, heavily clouded with slate underfur and of a cream or yellowish shade in some animals. Spinal stripe is most obvious in young individuals and in summer pelage and is frequently obscured in adults who have more dense black hairs. When present, the spine is usually restricted to mid-back and the rump. Winter fur is cream-white but hair bases remain slate; the head is darker than the back and a grey spinal stripe may be present. Feet and tail are grey. Skull is on average heavier and deeper than in *torquatus*. Molars are more complex with an additional postero-lingual vestigial angle T7 on M^1 and M^2, and a high frequency of the antero-labial vestigial angle (T5) on M_3 (Figure 21c–d). The karyotype ($2n=28$, $NF_a=50$) consists mainly of bi-armed chromosomes and is of the Beringian (=Nearctic) type (Kozlovsky 1974, Zima & Král 1984). Females have either XX or XY heterosomes (Fredga et al. 1999).

SUBGENUS: *Myolemmus* Pomel, 1852

Myolemmus Pomel, 1852:363. Type species: *Arvicola (Myolemmus) ambiguus* Pomel, 1852 [=*Dicrostonyx torquatus*; Trouessart 1897:547]; based on fossil material.

Synonyms. *Cuniculus* Wagler, 1830 [preoccupied]; *Misothermus* Hensel, 1855; *Borioikon* Polyakov, 1881; *Tylonyx* Schulze, 1897.

Taxonomy. The subgenus is generally known as *Misothermus* but the name is predated by *Myolemmus*. Contains a single polytypic species.

Characteristics. In addition to the nucleotide sequences (Fedorov et al., 2022), karyology provides the most distinguishing characteristic between subgenera: diploid number is high in *Myolemmus* and frequently contains additional B chromosomes.

Dicrostonyx torquatus (Pallas, 1779) – Siberian (Palaearctic) Collared Lemming

Taxonomy. In the past *torquatus* was frequently regarded as the only representative of the genus (Miller 1896, Ognev 1948).

Distribution (Figure 23). Endemic to the polar regions of the Russian Federation, from Mezen' River and the Kanin Peninsula (NE Arkhangelsk Oblast, European Russia) to Chukotka, the Bering Sea coast, and Kamchatka. Range covers 1,922,845 km² and extends in a narrow belt along the Arctic coast with southward expansions along the River Yenisey, in the north-eastern coast of the Sea of Okhotsk and in Kamchatka, reaching the southernmost point at 53⁰N latitude. Occurs on 7 islands (or island groups): Vaygach Island, Novaya

Zemlya (the Southern and Northern Islands), Belyy [=White] Island (near the northern end of the Yamal Peninsula), Severnaya Zemlya (Oktyabr'skoy Revolutsii [=Zemlya Imperatora Nikolaya II] and Bolshevik Islands), islands in the Lena River delta (Mostakh, Sagastyr and others), New Siberian Islands (quoted for the entire archipelago by Ognev 1948, but museum vouchers known only from Stolbovoy Island), and the Bear [=Medvezhyi] Islands (Chetyrekhstolbovoy Island). Possibly 70% of habitat was lost since the LGM (Fedorov et al. 2020). Major habitat is upland and well-drained treeless tundra and rocky alpine tundra; permafrost is frequently only 30–40 cm below the surface. Along the southern range margin, collared lemmings occupy sparse larch stands of the northernmost taiga belt but do not enter dark, closed-canopy taiga (Popov 1977). Recorded up to 1,400 m a.s.l. in the northern Ural Mts. and till 500–700 m in Kamchatka and Koryak Highland (Kostenko 1984).

Characteristics. General characteristics are the same as for the genus. Dorsal pelage is usually chestnut-brown, reddish-brown or with rich rusty shades on the anterior back, shoulders and front flanks; the combined effect of variously coloured hairs is a speckled pattern of blackish, light and rusty spots and patches (Figure 24a,b). The back is rarely plain (beige or ash-grey). Cheeks are buff, reddish-brown or grey; fur in front of pinnae is usually bright rusty and sharply contrasts a transverse light stripe behind the ears. Black spinal stripe is common but fades or disappears in the east. Belly is white and heavily washed by slate-grey undercolour; some animals show a buff tint. Tail is light grey above, whitish below; paws are whitish. Skull is essentially like in *vinogradovi*. Molar pattern is less complex and normally lacks vestigial angles T7 (on M^1–M^2), T6 (M_2) and T5 on M_3 (Figure 21a–a').

D. torquatus is polymorphic for a B chromosome system, hence the number of chromosomes in somatic cells varies from 46 to >80. Diploid complement (2n, without Bs) contains 45–48 mostly acrocentric chromosomes (NF=51–52; Gileva 1983), and the remaining 0–15 (possibly >30) elements are Bs. The presumed basic karyotype contains 48 ordinary autosomes and two heterosomes; translocations between autosomes led to a stepwise decrease in the diploid number (Fredga et al. 1999). Heterosomes are unusual since females possess either XX or XY complements and males have XY. Heterozygous females have X-linked mutation that supresses the Y chromosome (designated as X*) and converts such

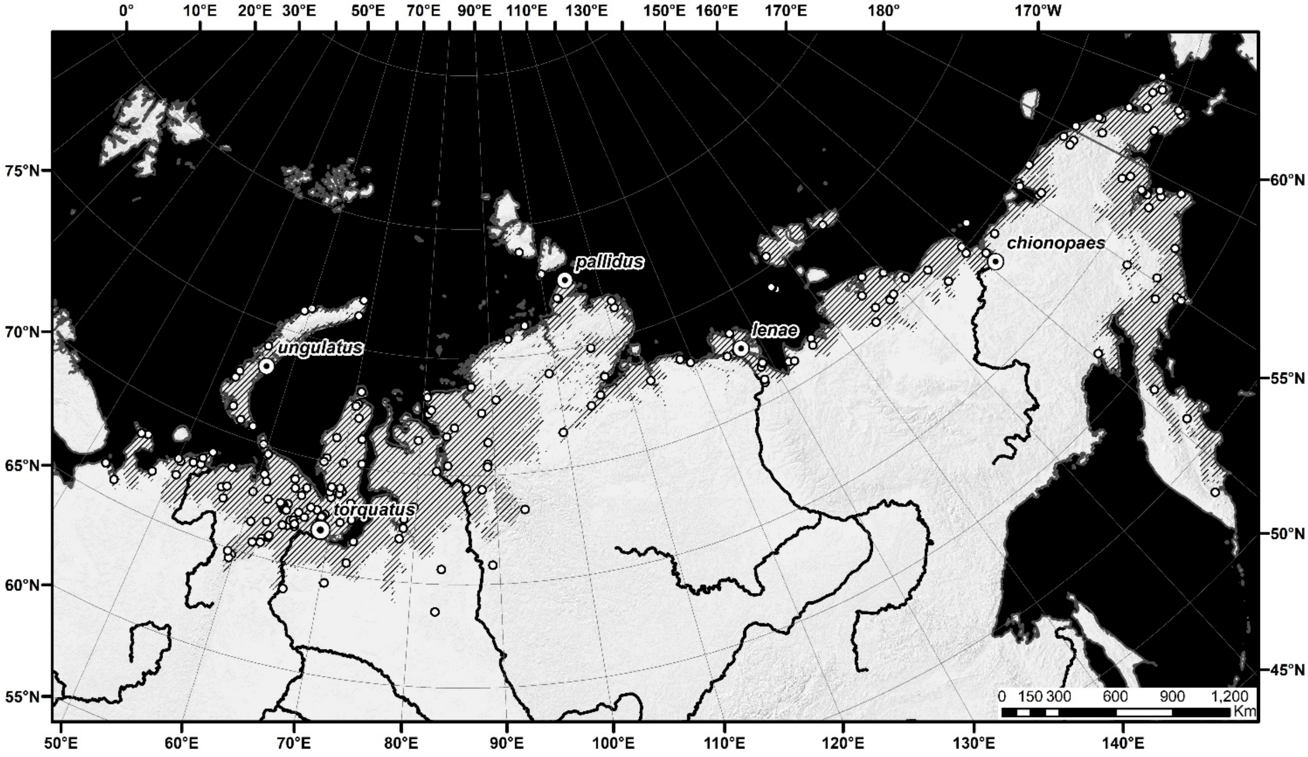


Figure 23: Distribution of the Siberian collared lemming *Dicrostonyx torquatus.*

individuals to females. Individuals from Chukotka and Polar Urals have 1 chromosome less in XY males and X*Y females than in XX and X*X females, the result of translocations between the Y and certain autosomes (Gileva 1983, Zima & Král 1984, Fredga 1988).

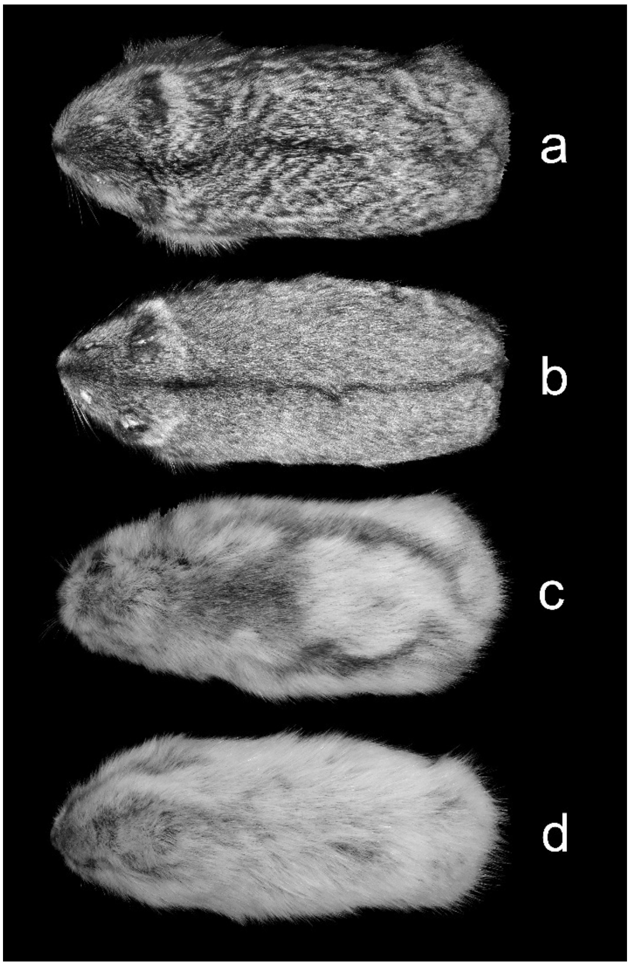


Figure 24: Individual and seasonal variation in fur colour of *Dicrostonyx torquatus.* Note the difference between dark summer (a,b–from the Timansky tundra) and white winter skins (c,d–Chukotka). Note the white "collar" behind the ears and the mid-spinal stripe in summer skins. Top winter skin (c) displays brown patches on shoulders and on sides of back; the individual on the extreme bottom (d) is plain white. Photo: B. Kryštufek.

Variation and subspecies. *Dicrostonyx* exhibits extensive chromosomal polymorphism with 4 races which are characterised by the morphology of heterosomes, by reduced chromosome numbers due to Robertsonian translocations and by the presence of supernumerary (B) chromosomes. These chromosomal races are congruent with the phylogeographic pattern of *Mt*-DNA. *Mt*-diversity is low between and within lineages (Fedorov et al. 1999) and becomes high to the east of Kolyma (West-Beringian lineage). Recent Siberian collared lemmings evolved from the West-Beringian lineage during the last 77 ky (CI=54–107 ky); the westernmost lineages (Pechora and Yamal) are <6.5 ka old (Fedorov et al. 2020). Over the last ~50 ky at least 4 different lineages succeeded each other across Europe and western Russia (Palkopoulou et al. 2016).

Traditional taxonomy recognised 1 island (*ungulatus*) and 2 mainland subspecies (Gromov et al. 1963, Gromov & Erbajeva 1985). Lemmings from Bolshevik Is. may represent another yet unnamed form (Gromov & Polyakov 1977). Colour varies clinally; in a west-to-east direction the rusty hues are replaced by a chestnut colour and the dark spinal stripe is gradually lost (Gromov & Polyakov 1977).

Dicrostonyx torquatus torquatus (Pallas, 1779)

Mus (torquatus) Pallas, 1779:77 + Table XI B. Type locality: "Novum hune praecedentis in Sibiria conterraneum postia notiorem faciam" and "hujus Sibirica fere minorem e regionibus ad Obum sitis arcticis accepi" (p. 206). Restricted to "Subarctic region of the Ob' estuary" (Ognev 1948:504), Siberia, Russian Federation.

Distribution. Arctic coast between the Kanin Peninsula and Yenisey.

Characteristics. Smaller than *pallidus*; skull is moderately deep. Dimensions: BWt=40–158 g, H&B=101–153 mm, TL=11–21 mm, HF=13–17 mm, EL=4–8 mm, CbL=27.2–23.7 mm, ZgW=17.6–22.6 mm, MxT=7.2–9.2 mm. Upper side is grey-brown, washed with rusty or buff shades; shoulders are the same colour as the back, flanks are reddish-brown, cheeks buff or reddish-brown; black spinal stripe is prominent. Contains 2 allopatric *Mt*-DNA sublineages (Fedorov et al. 1999) and a single chromosomal race (Race I; 2n=45–46 + 2–9 Bs; Fredga et al. 1999).

Dicrostonyx torquatus pallidus (Middendorff, 1852)

[Myodes torquatus] var. *pallida* Middendorff, 1852:93 (not 1867; Ognev 1948:506). Syntypes were captured in "Taimyrlande" (Taymyr Peninsula) and "Nówaja-Semljá" (Novaya Zemlya, Arctic Ocean, Russian Federation). Syntypes belong to two subspecies (the nominal and *ungulatus*). We therefore restrict the type locality to: Taymyr Peninsula, northern Krasnoyarsk Krai, Russian Federation.

Synonyms. *Mus lenae* Kerr, 1792; *Mus lenensis* Pallas, 1811; *Dicrostonyx chionopaes* G. M. Allen, 1914.

Distribution. From Taymyr Peninsula till Chukotka and Kamchatka.

Characteristics. Size large; skull shallow. Dimensions: BWt=47–153 g, H&B=109–155 mm, TL=14–22 mm, HF=14.5–17.0 mm, EL=4–7 mm, CbL=27.1–32.5 mm, ZgW=16.7–21.6 mm, MxT=7.3–8.8 mm. In captivity, *chionopaes* grow faster than the nominal subspecies (Prushinskaya et al. 1992). Size is stable among populations; CbL ($\bar{x}$ ±SD; mm) varies from 29.0±0.32 (lowlands along the Lena River) to 29.8±034 (Yamal) and 29.8±0.29 (Chukotka; Chernyavskiy 1984). Back is more variegated than in nominal subspecies; shoulders are richly rusty, cheeks grey, spinal stripe frequently ill-defined or absent. Animals from Taimyr are more blackish than those from Sakha and Chukotka (Chernyavskiy 1984). Karyotype: 2n=46, 47, 48 (Stenseth & Ims 1993). Contains 3 allopatric *Mt*-DNA sublineages centred in Taimyr, and in the deltas of Yana and Kolyma, respectively (Fedorov et al. 1999), and 3 chromosomal races (Fredga et al. 1999): Race II (2n=46 + 5–13 Bs), Race III (2n=37–39; without Bs), and Race IV (2n=47–48 + 3–6 Bs).

Dicrostonyx torquatus ungulatus (Baer, 1841)

Lemmus ungulatus Baer, 1841:283. Type locality: Island of Novaya Zemlya, Russia.

Distribution. Endemic to the Severny and Yuzhny Islands (Novaya Zemlya archipelagos, Arkhangelsk Oblast).

Characteristics. Cranially the most distinct subspecies with a deep skull and short nasals. Dimensions: H&B=131 mm, TL=25 mm, HF=15.5 mm, CbL=28.8–29.1 mm, ZgW=19.1–20.1 mm, MxT=4.6–7.8 mm. Externally similar to mainland lemmings. Pelage is ash-grey with a light brown shade and black spots; shoulders and front flanks are rusty-buff to chestnut-brown. A single *Mt*-haplotype is known which differs from the remaining conspecific sequences by 0.7–1.2% (Spitsyn et al. 2021b). Karyotype is not known.

TRIBE:
Lemmini Miller, 1896

Lemmi Miller, 1896:8. Type genus is *Lemmus* Link.

Synonyms. Hypudaei Fitzinger, 1867.

Taxonomy. The tribe contains 3 genera: *Lemmus*, *Myopus* and *Synaptomys*; the last holds a basal position in phylogenetic trees (Robovský et al. 2008).

Distribution. The range of the tribe is circumpolar, also encompassing boreal and temperate zones as far south as 45^0 north in Eurasia, and 35^0 north in North America (Shenbrot & Krasnov 2005). Of the 3 genera, *Lemmus* is Holarctic, *Myopus* is Palaearctic, and *Synaptomys* is Nearctic.

Characteristics. In the Palaearctic representatives the body is either vole-like (*Myopus*) or more chunky and robust (*Lemmus*); the tail is perpetually short (TL<HF), and terminates in a long pencil of stiff hairs. Head is rather large with a blunt snout; muzzle pad is obscure. Eyes are small and ears are normally developed though short. Although reduced in the majority of arvicolines, the thumb carries a large, blunt and flattened nail (Figure 25). The fur is long and dense. There are 8 mammae in *Lemmus* and *Myopus*; *Synpatomyx* has 6–8 nipples. Glans penis is cylindrical; baculum consists of a relatively short and robust proximal stalk and distal trident. The sperm head is falciform (Retzius 1909).

The skull is broad and low with powerful zygomatic arches which expand abruptly. Rostrum is relatively short, nasals are bottle-shaped. Interorbtital region is narrow with a prominent ridge which expands posteriorly across temporals, reaching the lambdal crest. Post-orbital process on the squamosal is evident but less prominent than in *Dicrostonyx*. Maxillary tooth-rows rapidly diverge posteriorly. Incisive foramina are rather short and wide; the lateral palatal grooves are well-marked. Posterior edge of the hard palate terminates into a transverse shelf and covers post-palatal pits; median spine is short but prominent (Figure 10c). Pterygoid processes are heavy, interpterygoid space is

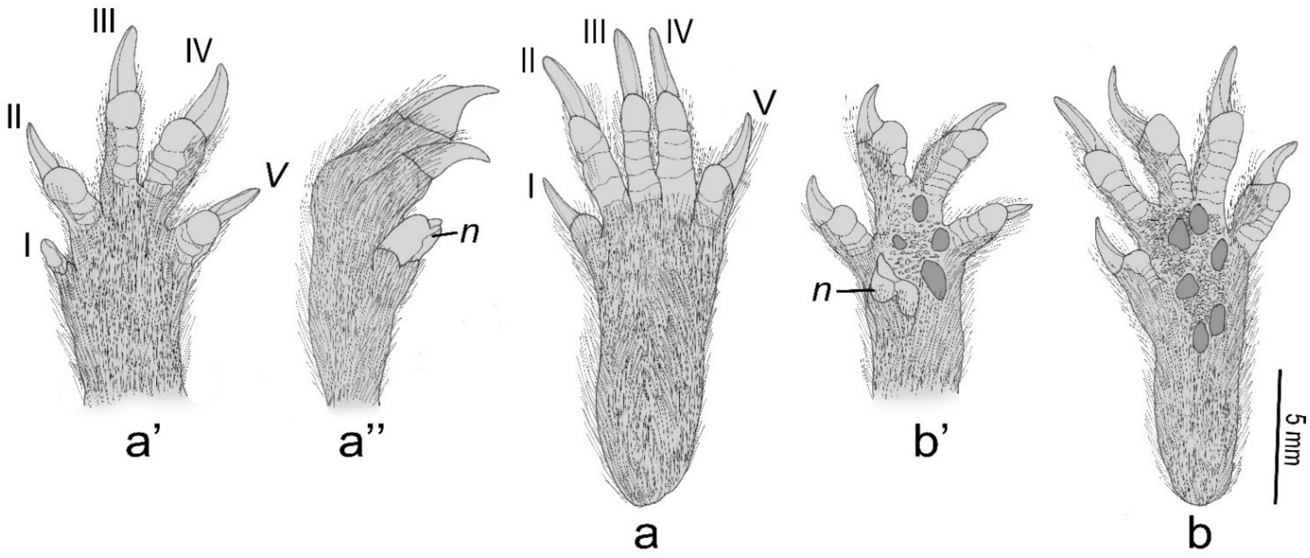


Figure 25: Palm (a',b'–ventral, a''–lateral) and solve (a,b) in *Lemmus lemmus lemmus* (a) and *Myopus schisticolor* (b). *n*–a large flattened nail on the thumb.

wide. Bullae ovate, mastoid portion slightly inflated. Dorsal profile flat except in the nasal region which bends downward abruptly. Mandible is rather slender; coronoid process is short and blunt.

Upper incisors are weak relative to the skull, sometimes with a shallow groove. Lower incisors are of the lemming type, i.e. short (terminating anterior to or below M_3) and placed on the lingual side of the molar row. Molars are hypselodont with cement in re-entrant folds. The enamel band is interrupted by dentine tracks at the apex of each salient angle. Schmelzmuster is differentiated into leading and trailing edges which are of approximately the same width (0.04 mm in *Myopus* and 0.05–0.06 mm in *Lemmus*). The leading enamel edge consists of 2 layers (the inner lamellar and the outer radial) while the trailing edge has 3 layers (the inner radial and 2 lamellar layers; Koenigswald & Martin 1984). Lingual salient folds are broadly truncated in all upper molars and are therefore smaller than the labial. In the upper row, M^1 and M^2 have 4 and 3 triangles, respectively, posterior to the anterior loop. M^3 is distinctive as the triangles merge into nearly transverse laminas; the posterior loop is simple. In lower molars, the salient angles are truncated on the labial side of M_3 and on the posterior loop in the remaining molars. M_1 consists of the anterior loop and the trigonid-talonid complex; M_2 has 4 alternating triangles and the posterior loop; M_3 is characterised by a vestigial antero-labial triangle (T2) and a large transverse posterior loop. Lemmings are unique among arvicolines because of long M_2 and M_3 relative to M_1 (Renvoisé et al. 2009).

Key to genera and species

1a) Ventral side dark grey (slate); palms and soles with distinct tubercles; M^3 relatively narrower ……….. ....*Myopus schisticolor*
1b) Ventral side whitish, light-grey, buffy or rusty; palms and soles densely hairy throughout, tubercles rudimentary; M^3 relatively wider ………..….2 (*Lemmus*)
2a) Mid-dorsal black stripe present in young, frequently also in adults; all chromosomes acrocentric, Y chromosome short (~½ the size of the X) ….. *L. lemmus*
2b) Mid-dorsal streak absent; at least 1 autosomal pair is bi-armed; Y chromosome longer (~3/5 the size of the X) ……………………………………………….. *L. nigripes*

GENUS: *Lemmus* Link, 1795 – Brown Lemmings

Lemmus Link, 1795:75. *Mus lemmus* Linnæus is the type by absolute tautonomy.

Synonyms. *Myodes* Pallas, 1811; *Hypudaeus* Illiger, 1811; *Brachyurus* Fischer, 1813; *Lemnus* Kretzoi & Kretzoi, 2000.

Taxonomy. Cranially and dentally similar to *Myopus*, but the two differ in external appearance and configuration of palms and soles. *Lemmus* and *Myopus* are in a sister position (Steppan & Schenk 2017).
Number of species recognised in the Palaearctic *Lemmus* varied between 1 species (Sidorowicz 1964) and 6 species (Spitsyn et al. 2021a). We advocate a 2-species

Figure 26: Palaearctic brown lemmings (*Lemmus lemmus*): a–ssp. *lemmus* (Femundsmarka National Park, Norway); b–ssp. *sibiricus* (Taimyr, Russian Federation). Photo courtesy Miloš Anděra (a) and Sim Broekhuizen (b).

division which is in agreement with the evidence from cross-breeding experiments (Rausch & Rausch 1975, Pokrovski et al. 1984, Kuznetsova et al. 1993), karyotypes (Gileva et al. 1984, Stenseth & Ims 1993) and phylogenetic reconstructions (Fedorov et al. 2003, Abramson & Petrova 2018).

Distribution. Zones of Holarctic taiga and tundra. *Lemmus* does not penetrate as far north as *Dicrostonyx*, hence it is absent from many islands in the Arctic Ocean (incl. Greenland). The southern border is near the 50th northern parallel in the mountainous regions of eastern Asia.

Characteristics. Small to medium sized true lemmings of chunky appearance (Figure 26). The head is relatively large, broad and flattened with small eyes and short, tufted ears which are hidden in the fur. The pinna is normally developed but smaller than in *Myopus*. A small tragus and antitragus are separated by a deep intertragal notch (Figure 27). Legs are short and muscular, paws broad and densely clad with stiff hairs; palmar and plantar pads are vestigial. Fingers are short and stout; the palmar thumb is very short. Claws are heavier on front fingers but are of approximately the same length as on hind fingers. Palmar claws are thicker in winter (November–July) than in summer (July–October). Metacarpals III and IV are shorter than phalanges; terminal (ungual) phalanges of manus are enlarged (longer than corresponding 1st and 2nd phalanges combined; Miller 1912a). Tail is slightly shorter than hind foot, club shaped, densely haired with a long terminal pencil (Figure 28). Fur is dense, soft and long, monochromatic or with light- and dark-coloured spots; mid-spinal stripe may be present. Baculum is of the arvicoline type; the proximal stalk has a broadly expanded base (see under species).

Skull is described above under the Lemmini tribe (Figures 29, 30). Dental pattern (Figure 31) is essentially as in *Myopus*; the anterior loop of M_1 tends to be longer and the posterior loop of M_3 is in general more robust and longer in *Lemmus* (Ponomarev et al. 2013). In the Far East (*Lemmus lemmus amurensis*), the ratio of the width of M^3 with length as a denominator is 0.47–0.59 (versus 0.58–0.71 in *Myopus;* Tiunov & Panasenko 2010).

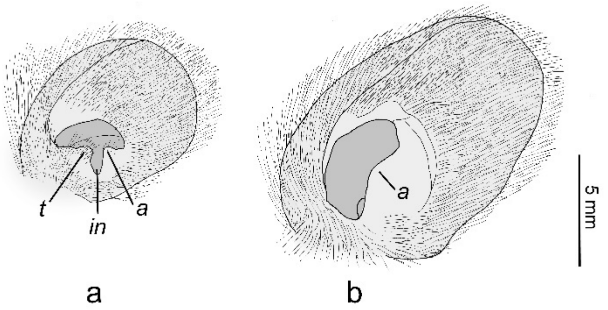


Figure 27: Left pinna in *Lemmus lemmus lemmus* (a) and *Myopus schisticolor* (b). The meatus is shaded dark. Abbreviations: *a*–anitragus, *in*–intertragal notch, *t*–tragus.

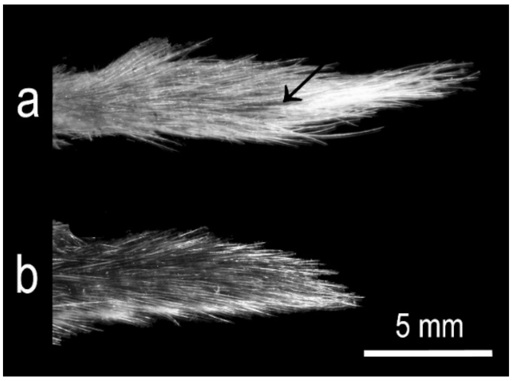


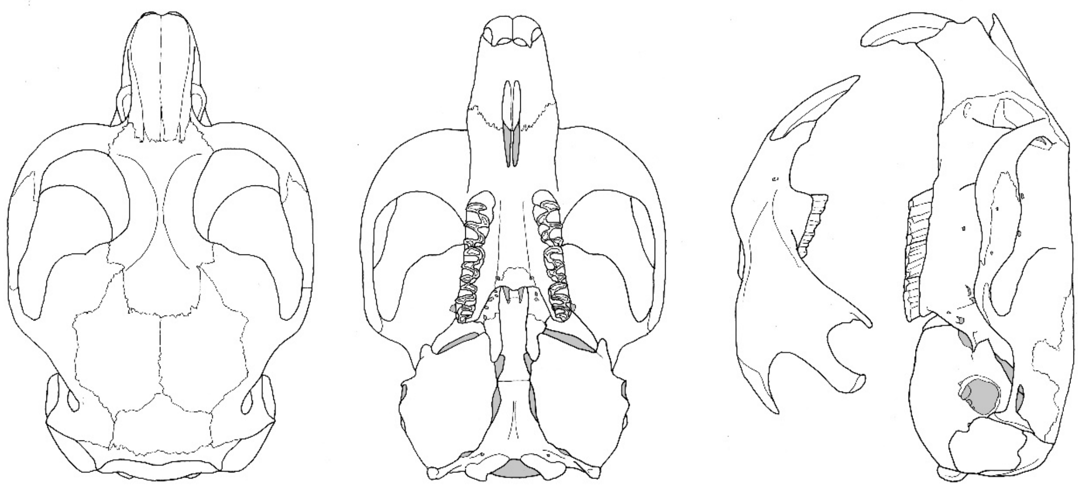
Figure 28: Tail in *Lemmus nigripes* (a–Alaska, USA) and *Myopus schisticolor* (b–Murmansk District, Russian Federation). Arrow points to the tip of caudal vertebrae.

Lemmus lemmus (Linnæus, 1758) – Palaearctic Brown Lemming

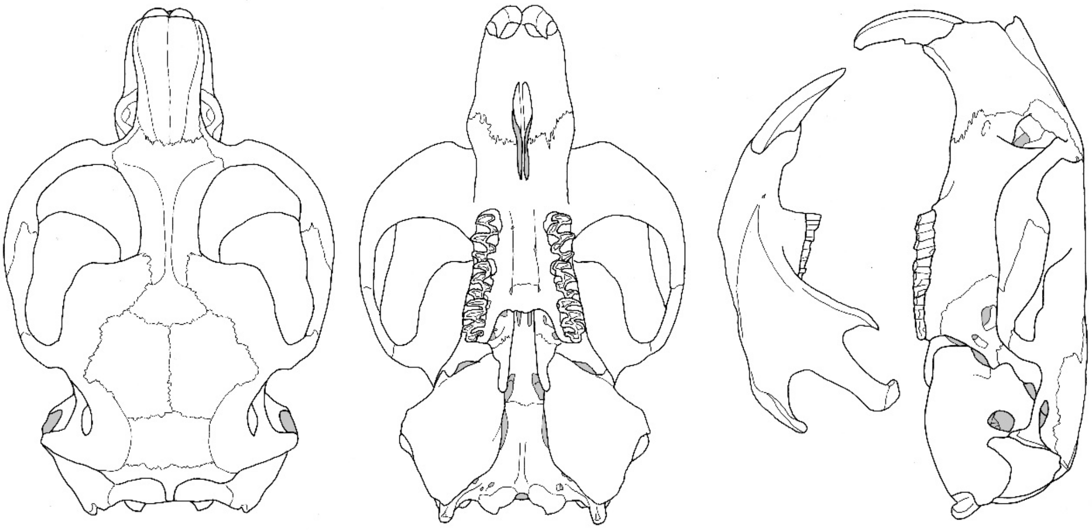
Taxonomy. As understood here, *L. lemmus* contains Palaearctic brown lemmings other than *L. nigripes* which are at present classified as 3 species (*lemmus, sibiricus, amurensis*; Pardiñas et al. 2017). These taxa are closely related and produce fertile offspring; moreover, *sibiricus* and *amurensis* are paraphyletic in phylogenetic trees. Morphological diversity in the group cannot be linked to genetic heterogeneity and is presumably of relatively recent origin.

Distribution (Figure 32). Similar to the genus but absent east of Kolyma–north-eastern Sea of Okhotsk; present in Kamchatka. Distributional range measures an estimated 1,953,720 km^2. Widely sympatric with *Dicrostonyx* but prefers more humid habitats. Elevational range is from sea level up to 1,760 m.

L. l. lemmus



L. l. sibiricus



L. l. novosibiricus

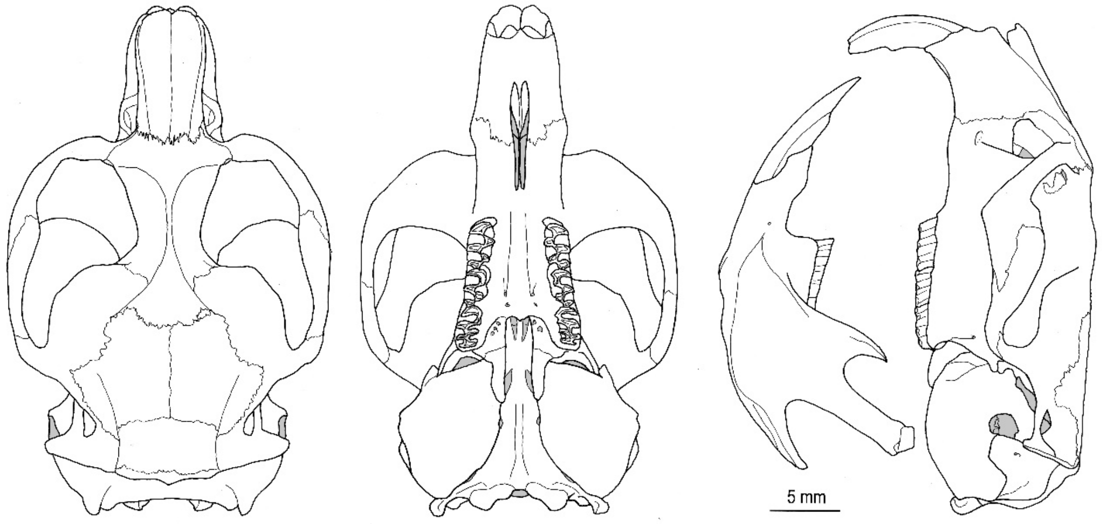
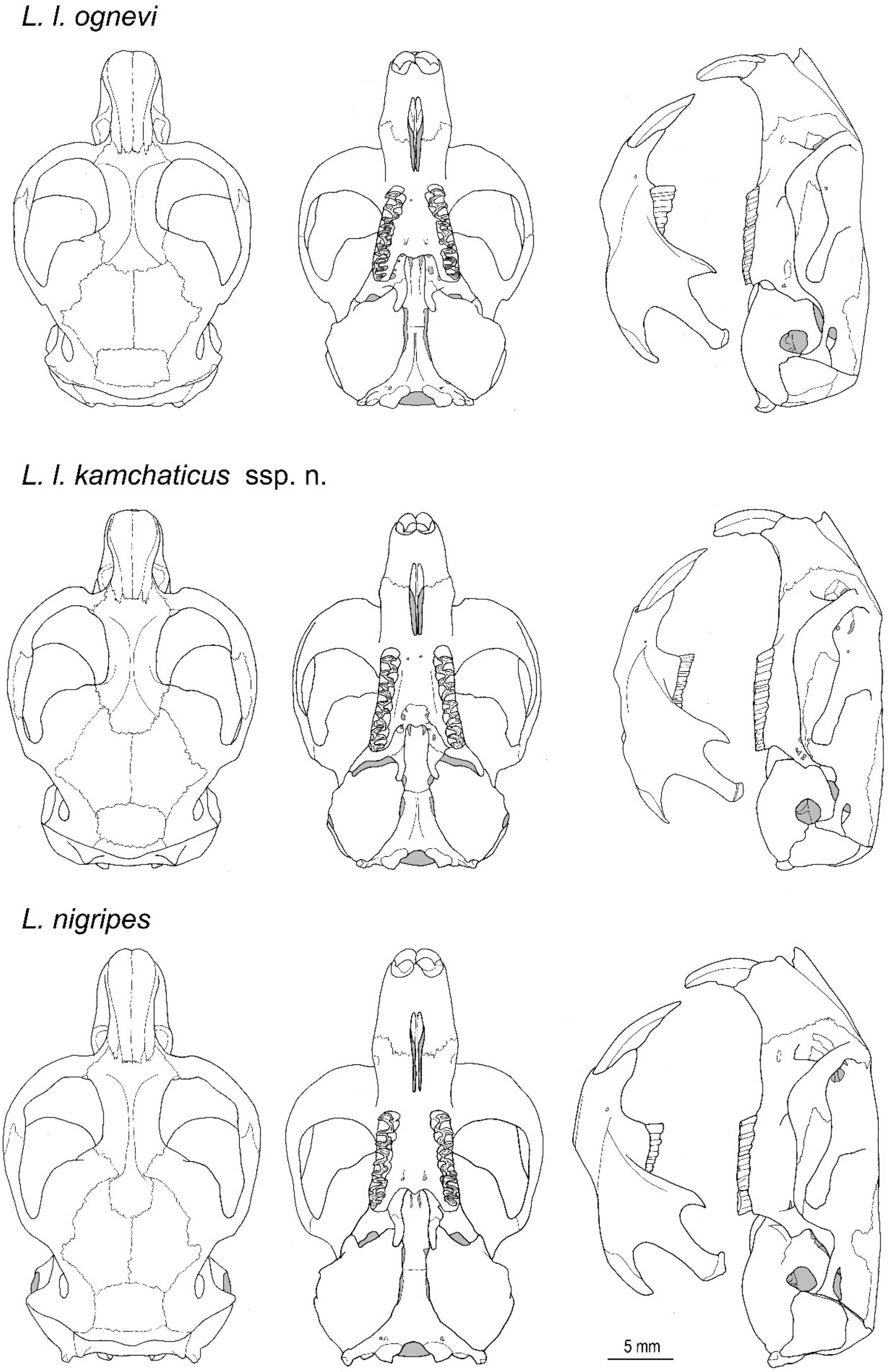


Figure: 29: Skull and mandible in Palaearctic brown lemmings (*Lemmus lemmus*). Top to bottom: *L. l. lemmus* from Kuusamo, Oulanka, Rusppilampi, Finland; *L. l. sibiricus* from Chelyuskin, Taymyr, Krasnoyarsk Krai, Russian Federation; *L. l. novosibiricus* from Wrangel Island, Chukotka Autonomous Okrug, Russian Federation.



L. l. ognevi

L. l. kamchaticus ssp. n.

L. nigripes

Figure 30: Skull and mandible in brown lemmings (*Lemmus*; all from Russian Federation). Top to bottom: *L.lemmus ognevi* from the Basin of the Aldan River, Sakha Oblast; *L.lemmus kamchaticus* from Lake Maloe, Kamchatka, Russian Federation; *L. nigripes* from Anyuy Mts., right bank of River Kolyma, Russian Federation.

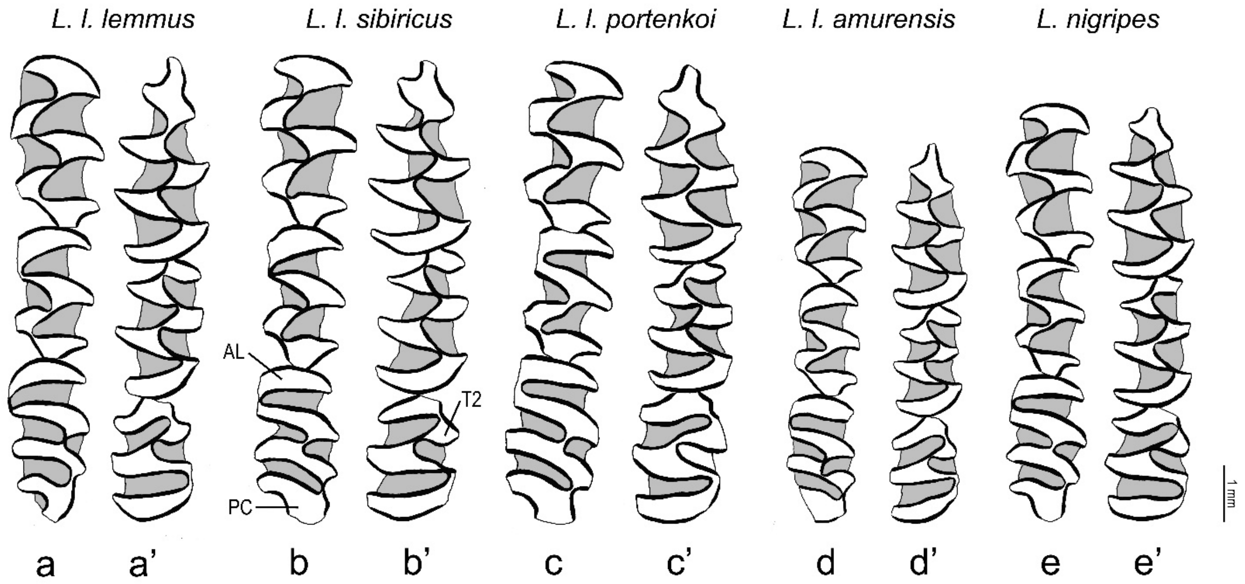


Figure 31: Molar grinding pattern of the upper and lower molars in true lemmings (*Lemmus*): a–*L. l. lemmus* from Kuusamo, Oulanka, Rusppilampi, Finland; (b) *L. l. sibiricus* from Yamal, Russian Federation; c–*L. l. portenkoi* from Wrangel Island, Chukotka Autonomous Okrug, Russian Federation; d–*L. amurensis* from Pikan, 15 km south-east of Zeya, Amur Oblast, Russian Federation; e–*L. nigripes* from Chaun River, Eastern Siberia, Russian Federation.

Characteristics. Similar to the genus. Morphological variability is excessive (Figure 33) and is detailed in the account on subspecies. All chromosomes are acrocentric (2n=NF=50); the X is large and the Y is small or medium-sized. No substantial variation in conventionally stained and C-banded chromosomes was recorded between *lemmus, sibiricus*, *novosibiricus*, *portenkoi*, and *amurensis* (Kozlovsky 1974, Rausch & Rausch 1975, Gileva 1983, Zima & Král 1984).

Variation and subspecies. Major genetic divergence (net divergence=3.8±0.6%; Fedorov et al. 2003) is tentatively at the Lena River. This dichotomy marks 2 subspecies groups, the western (*lemmus*) group and the eastern (*amurensis*) group.

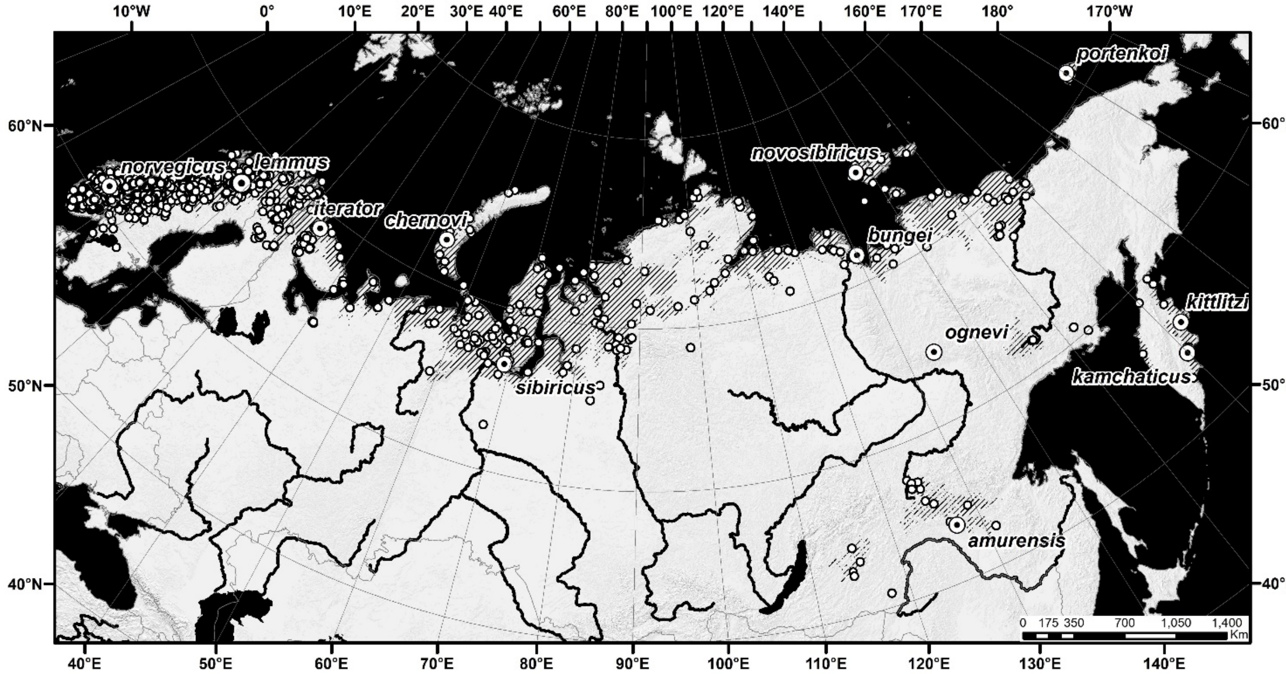


Figure 32: Distribution of the Palaearctic brown lemming *Lemmus lemmus*.

Subspecies group *lemmus*

The group comprises *Mt*-phylogeographic lineages of the Western group (sensu Fedorov et al. 2003) and occurs west of the Lena River. These lemmings do not have a rusty muzzle.

Lemmus lemmus lemmus (Linnæus, 1758)

Mus lemmus Linnæus, 1758:59. Type locality ("Habitat in alpibus Lapponicis") restricted to Virijaure, Sweden (Wallin 2001:47).

Synonyms. *Mus Lemmus, norvagicus* Pallas, 1779; *Lemmus borealis* Nilsson, 1820; *Lemmus norvegicus* Desmarest, 1822; *Cuniculus iterator* Gistel, 1850; *Myodes lemmus* var. *crassidens* Nehring, 1899.

Taxonomy. Because of its unique colouration, subspecies *lemmus* is uniformly accepted as a species in its own right and endemic to Fennoscandia; Sidorowicz (1964) and Lissovsky et al. (2019) are the only authors who opposed this view. The divergence time between *lemmus* and *sibiricus* is <80ky (Langerholm et al. 2014). Controlled crossbreeding trials yielded fertile offspring with subspecies *sibiricus, amurensis, portenkoi,* and *kamchaticus* new subspecies (Pokrovski et al. 1984, Kuznetsova et al. 1993).

Distribution. The Fennoscandian Peninsula in Norway, Sweden, northern Finland, and northern Kola Peninsula (Russia). Islands are inhabited only to the north of the Arctic Circle. The range covers 550 thousand km^2 in alpine and subarctic tundra from sea level till 1,760 m a.s.l. Main habitats during summer are "wet, often paludified areas on bogs or close to open water" while a drier snow bed vegetation is colonised in winter. At intervals >30 years lemmings disperse en mass from mountain tundra invading >200 km deep into taiga, reproduce there for 2–3 years, and then experience an extirpation events (Stenseth & Ims 1993).

Characteristics. A large subspecies, unmistakably recognisable by its brilliant pelage (Figures 26a & 33). Dimensions: BWt=36–104 g, H&B=105–155 mm, TL=12–26 mm, HF=13–22 mm, EL=7.5–12 mm, CbL=25.2–33.7 mm, ZgW=15.8–23.2 mm, MxT=6.2–8.6 mm. Top of head, neck, withers, shoulders and front back are black, posterior back is ochraceous or tawny, occasionally with a black streak extending till the rump (present in ~80% of individuals); rump and flanks are black in ~75% of animals. Contrasting paired light blotches around ears are particularly characteristic. Muzzle is white or buff but never rusty. Underparts are beige, paler on throat and chin, cheeks are yellow. Hair bases are slate except on lips and chin. Feet are whitish or buff with nearly blackish distal part; tail is greyish buff, terminal pencil is whitish or buff. Colour varies individually and also depends on age. Dimensions (width×depth of the claw on thumb III) in summer/winter claws are: 0.80–1.20×0.96–1.73 / 1.30–1.59×2.04–2.67 mm. Baculum: the medial distant element is nearly as long (=1.45 mm) as the proximal bone (=1.90 mm). Base of the proximal baculum is widely expanded; lateral distal bones are moderately long (=0.78 mm) and weak.

Lemmus lemmus chernovi Spitsyn, Bolotov & Kondakov, 2021

Lemmus lemmus chernovi Spitsyn, Bolotov & Kondakov, 2021a:105. Type locality: "Russia, Novaya Zemlya, Southern Island, near Malye Karmakuly Polar Station, 72.3822°N, 52.7506°E, altitude 17 m, wet saxifrage-roseroot communities".

Taxonomy. Presumably isolated from the Fennoscandian subspecies for 93 ky (CI=38–170 ky; Spitsyn et al. 2021a).

Distribution. Novaya Zemlya archipelagos, Russia. Subspecific identity known with certainty for the Southern Island.

Description. Combines the genetic makeup of subspecies *lemmus* with the pelage colouration of *sibiricus*. Dorsal hairs are reportedly more yellowish in *chernovi* and more brownish in *sibiricus*. Dimensions: H&B=125–145 mm, TL=12–15 mm, HF=14–16 mm, CbL=30.4–32.7 mm, ZgW=21.2–23.4 mm, MxT=8.2–8.9 mm (Spitsyn et al. 2021a).

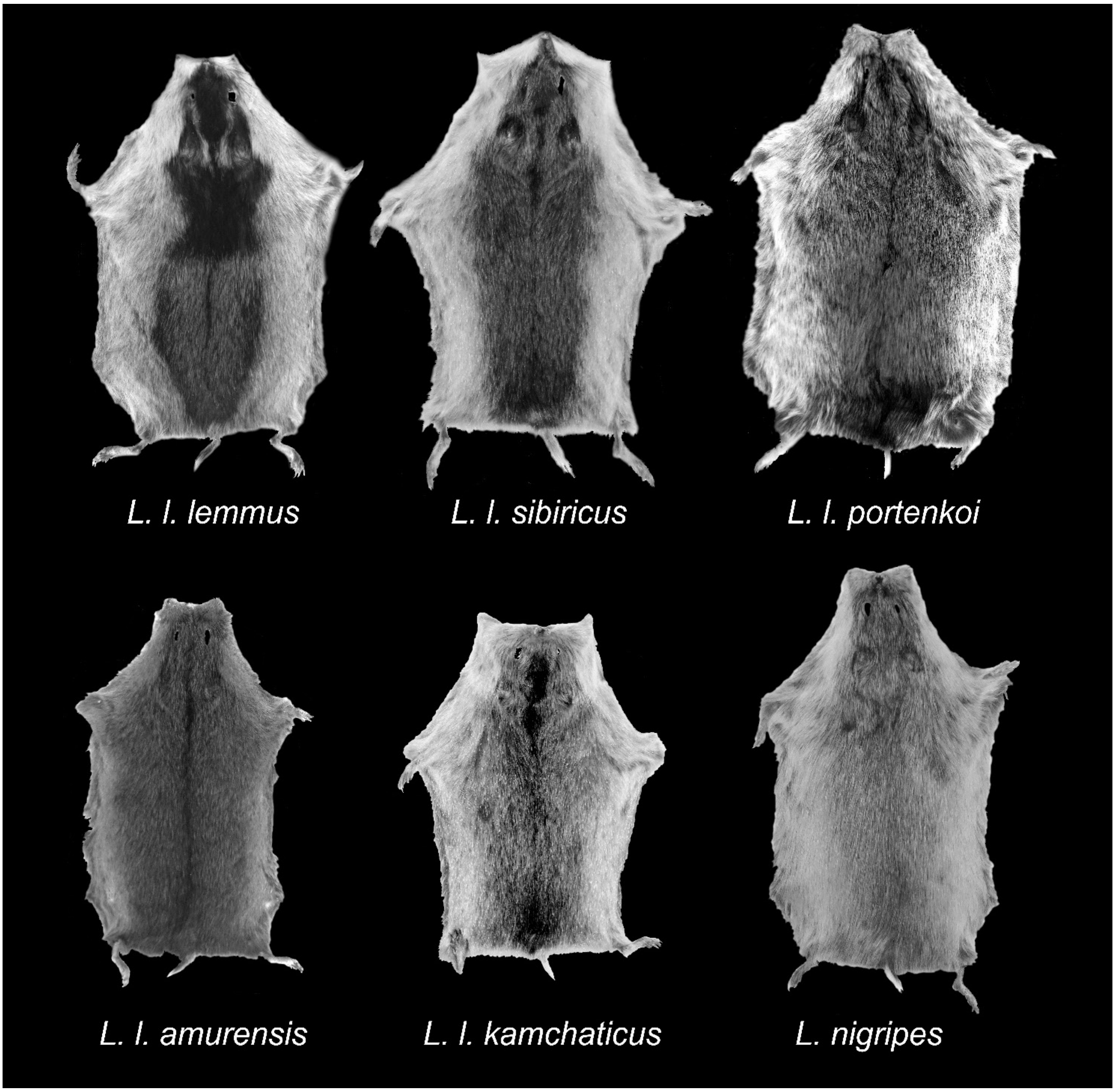


Figure 33: Skins of brown lemmings (all from Russian Federation; left-to-right and top-to-bottom): *Lemmus lemmus lemmus* (Kola); *L. l. sibiricus* (lowlands along the Ob' River); *L. l. portenkoi* (Wrangel Island); *L. l. amurensis* (southern Sakha); *L. lemmus kamchaticus* ssp. n. (Kronotsky Zapovednik, Kamchatka); *L. nigripes* (Chukotka). Photo: Boris & Alenka Kryštufek.

Lemmus lemmus sibiricus (Kerr, 1792)

Mus Lemmus sibiricus Kerr, 1792:241. Type locality: "northern parts of the Uralian chain of mountains, and on the River Oby [Ob']", Russian Federation.

Synonyms. *Mus lemmus variegatulus* Pallas, 1779 [nomen oblitum]; *Lemmus obensis* Brants, 1827; *Lemmus obensis bungei* Vinogradov, 1924.

Taxonomy. Referred to as *obensis* in older literature. Fredga et al. (1999) defined *sibiricus* within the same geographic scope as here but ranked it as a species in its own right. The majority of other authors used *sibiricus* (or *obensis*; Ognev 1948) for lemmings from the shores of the Arctic Ocean between the Northern Dvina and Kolyma Rivers (Gromov & Erbajeva 1995, Pavlinov et al. 2002), sometimes with the inclusion of populations from Chukotka and Kamchatka (Ognev 1948, Pavlinov

& Rossolimo 1987). Ellerman & Morrison-Scott (1951) included all Palaearctic lemmings in *sibiricus* except those from Fennoscandia (*lemmus*). Controlled crossbreeding trials yielded fertile offspring between *sibiricus* and *lemmus, amurensis, portenkoi,* and *kamchaticus* n. ssp. (Pokrovski et al. 1984, Kuznetsova et al. 1993).

Distribution. The shores of the Arctic Ocean, between the Northern Dvina and Lena Rivers; present on Vaygach Island. Southernmost records are at 65° northern latitude in the polar Ural Mts. The range measures 931 thousand km^2. Main habitat is swampy lowland tundra with abundant grass, sedges, dwarf willows and rocky habitats with lichens and mosses in the uplands (up to 800 m a.s.l.); winter is spent under permanent snow cover in mossy areas with dwarf birch (Popov 2017). Tundra on loose soil with a turf of various types of grasses and mosses is preferred (Sdobnikov 1957). In the West Siberian lowland, the vast majority (94%) of lemmings occur in various types of subarctic tundra, mostly (89%) in the northern moss subzone of subarctic tundra. Further south, lemmings are rare in open canopy taiga and absent from dark taiga woodland (Kislyi et al. 2019).

Characteristics. Large lemmings with "monochromatic" pelage (Figure 33). Dimensions: BWt=49–120 g, H&B=99–154 mm, TL=12–24 mm, HF=15–20 mm, EL=7.5–12 mm, CbL=28.4–35.6 mm, ZgW=19.7–24.5 mm, MxT=8.0–10.0 mm. Dorsal pelage is brown with buff, rusty or grey shades. General impression is rusty but this varies among individuals and populations. Some lemmings are more buff and still others are beige; belly is whitish-grey, grey or washed buff or cream and the demarcation on flanks is distinct. Cheeks and the auricular area are black in some animals while others may have a buff subauricular tuft. Hind foot (normally grey or brownish throughout) has a blackish tarsum and fingers in the majority of lemmings from Yamal. Muzzle is whitish, grey or light buff but never rusty. Black spinal stripe is always present but is frequently (45% of individuals) restricted to the anterior part (head and neck); in ~5% of lemmings the stripe is restricted to the head, from the nasal to occipital region. In the remainder, the stripe is bold on the head and rump, but fades on the mid-back. The rump is the same colour as the back (~45% of lemmings) or black. Juveniles are similar in colour to adults. Length of dorsal (ventral) hair is 11.5–12 (6–6.5) mm in summer and 14–18.5 (7–10) mm in winter. Length of tail pencil is 6.5–8.3 mm. Dimensions (width×depth of a claw on thumb III) in claws are: 0.86–1.28×1.08–1.74 mm (summer) and 1.15–1.96×2.03–2.91 mm (winter). Skull is well-ridged with expanded zygomatic arches (ZgW/CbL=0.65–0.72); auditory bullae are rather small (Figure 29). Dentition shows no peculiarities (Figure 31b).

Subspecies group *amurensis*

The group comprises *Mt*-phylogeographic lineages of the Central group (sensu Fedorov et al. 2003) and occurs east of the Lena River. The oral region of the muzzle is frequently rusty.

Lemmus lemmus amurensis Vinogradov, 1924

Lemmus amurensis Vinogradov, 1924:186. Type locality: "Pikan, on Zeya River, a tributary of Amour [Amur River], East Siberia", Russian Federation.

Taxonomy. The majority of authorities accepted *amurensis* as a species in its own right, usually with the inclusion of *ognevi* (Corbet 1978, Pavlinov & Rossolimo 1987). In the opinion of some authors, *amurensis* also includes *chrysogaster* (Pavlinov & Lissovsky 2012), *novosibiricus* and part of *chrysogaster* (Musser & Carleton 2005); still others synonymised *amurensis* with *sibiricus* s.lat. (Honacki et al. 1982). We accept the taxonomic scope as defined in Lissovsky et al. (2019). Crossbreeding trials yielded fertile offspring between *amurensis* and *lemmus, sibiricus, portenkoi,* and *kamchaticus* ssp. n. (Pokrovski et al. 1984, Kuznetsova et al. 1993).

Distribution. Inside the triangle formed by the Vitim Plateau (Chita)–middle course of the Amur River (Zeysky District)–upper course of the Aldan River and measures 117 thousand km^2. The range is isolated from the nearest conspecific population (*ognevi*) by a gap ~1000 km wide. Living south of permafrost, *amurensis* occupies paludified mossy and scrubby areas with a high water table. The habitat may remain frozen over a sequence of years (Krivosheev 1986). Found up to 1,330 m a.s.l.

Characteristics. A small and brightly coloured lemming (Figure 33). Dimensions: BWt=37.5–51 g, H&B=107–119 mm, TL=9–14 mm, HF=14–16 mm, EL=9.8–11.5 mm, CbL=24.9–28.0 mm, ZgW=15.6–18.9 mm, MxT=6.9–8.1 mm (Chernyavskiy 1984). Dorsal pelage is russet, rusty-brown or wood-brown; oral region of the snout is always tawny. Cheeks, side of the neck and shoulders are the same colour as the back; flanks are cinnamon-rufous and the transition is blurred. Belly is ochraceous-tawny and clouded by slate underhair; some individuals have white hair on the chin. Occasionally, a rusty subauricular tuft is present. Some individuals are more brightly rufous (lighter ventrally) and still others are more buffy. Individuals from the Khabarovsk region are duller and do not have rusty cheeks but the muzzle is invariably reddish. Mid-dorsal black stripe extends from front to rump but is shorter or entirely absent in some individuals. The stripe is boldest on the head-top and the neck and less distinct posteriorly. A black patch on the rump is present in approximately half of animals. Tail is sharply bi-coloured: tawny above, white below; terminal tuft (length=3.5–5.5 mm) is all-white. Feet are grey with stiff whitish hairs on palms and soles.

Lemmus lemmus novosibiricus Vinogradov, 1924

Lemmus obensis novosibiricus Vinogradov 1924:187. Type locality: "Islands Kotelny and Liakhov [Lyakhov], New Siberian Archipelago N.E. Siberia", Sakha Republic, the Russian Federation; restricted to Kotelny (Pavlinov & Rossolimo 1987:207).

Distribution. Arctic tundra between the Lena and Kolyma Rivers. The eastern border is tentative since no lemmings have been screened for their genetic makeup between the Lena and Yana Rivers. Also present on the New Siberian archipelagos (Little and Great Lyakhovsky Islands, Kotelny, and Novaya Sibir) and Madvezhyi (Bear) Islands. Distributional range covers an area of 356 thousand km^2 and elevational range is from sea level up to 1,350 m. Main habitat is flat and moist Arctic tundra with mires and bogs; in the lowlands along the Kolyma River it occupies coniferous forests of the taiga type (Tavrovskiy et al. 1971).

Characteristics. Large lemmings (Figure 33), similar to ssp. *sibiricus*, but with the oral portion of muzzle contrastingly rusty (snout is white or beige in <10% of animals). Dimensions: BWt=51–108 g, H&B=91–165 mm, TL=8.5–23 mm, HF=14.8–19 mm, EL=6.5–14 mm, CbL=27.8–38.2 mm, ZgW=16.8–25.2 mm, MxT=7.8–12.0 mm. Colour as in *sibiricus*; some individuals are darker. The stripe, although present in the majority of animals (absent in ~10%), is complete only in ~20% of individuals. Rump is always black. Lemmings from the New Siberian Islands are larger ($\bar{x}$ CbL=34.5 mm vs 31.2 mm on the mainland) and have grey cheeks; grey tints spread backwards to the anterior half of the body. The rest of the back is rusty (rarely buffy). Spinal stripe is present but usually restricted to the anterior part. Winter pelage (length of fur=28 mm) is between pinkish buff, smoke grey and light drab; flanks are greyer, belly is grey with buff shades.

Lemmus lemmus ognevi Vinogradov, 1933

L.[emmus] a.[murensis] ognevi Vinogradov, 1933:58. Type locality: "Verkhoyansk ridge"; subsequently restricted to: "Yakutsk ASSR [now Yakutsk Republic or Sakha], upper reaches of R.[iver] Nel'gese (= Nel'chekhe)" (Pavlinov & Rossolimo 1987:206).

Synonyms. *Myodes Kittlitzii* Brandt, 1845 [nomen nudum]; *Myodes Kittlitzii* Middendorff, 1852 [nomen oblitum].

Taxonomy. Described as a subspecies of *amurensis* and frequently treated as such (Musser & Carleton 2005); Fredga et al. (1999) classified *ognevi* as a subspecies of *bungei*. In the molecular tree, *ognevi* holds a sister position to the clade of *novosibiricus* + *portenkoi* + *kamchaticus* ssp. n. (Abramson & Petrova 2018).

Distribution. Known from a handful of localities east of the mid-Lena River in the upper courses of the Yana, Kulu and Omolon Rivers; there is an isolate in northern Kamchatka (Ust'Kamchatsk). The range is south of the permafrost zone; habitat requirements are similar to those of *amurensis* (Krivosheev 1986).

Characteristics. Small lemmings; pelage is never as bright-russet as in *amurensis*. Dimensions: BWt=13.1–50.9 g, H&B=90–110 mm, TL=10–16 mm, HF=12–15 mm, EL=6–9 mm, CbL=23.3–25.5 mm, ZgW=15.0–17.0 mm, MxT=7.0–8.5 mm. Dorsal pelage is brown and shaded either grey, blackish, buff or rusty. The muzzle and hair around the pinnae are invariably rusty. The spinal stripe usually extends from nose to rump; it is frequently bold, particularly on the head, neck and shoulders; occasionally the stripe is absent. Flanks vary from grey to buff and cheeks are light fawn. Ventral side is plain grey, occasionally shaded buff; the transition on the flanks is blurry. A black spot on rump can be extensive but is not present in all animals. Feet are grey and claws are amber; palms and soles are less hairy than in lemmings from the Arctic tundra. Tail is buff all-around; the terminal tuft (length=3.2–4.3 mm) is white. Apart from its small size, the skull shows no peculiarities (Figure 30); zygomatic arches are well-expanded (ZgW/CbL=0.63–0.69).

Lemmus lemmus portenkoi Tchernyavsky, 1967

Lemmus sibiricus portenkoi Tchernyavsky, 1967:1865. Type locality: "Island Wrangel, vicinity of Mt. Tundrova", Arctic Ocean, Far Eastern District, Chukotka Autonomous Okrug, the Russian Federation.

Taxonomy. Commonly classified as a subspecies of *sibiricus* s.lat. (Gromov & Polyakov 1977, Pardiñas et al. 2017), of *bungei* (Fredga et al. 1999) or tentatively of *trimucronatus* (Pavlinov 2006); rarely treated as a species in its own right (Musser & Carleton 2005). Phylogenetic reconstruction suggests close relationships between *portenkoi* + *novosibiricus* + lemmings from south-eastern Kamchatka (Abramson & Petrova 2018). Offspring with *lemmus, sibiricus, amurensis,* and *kamchaticus* ssp. n. are fertile (Pokrovski et al. 1984, Kuznetsova et al. 1993).

Distribution. Endemic to Wrangel Island. Habitat is moderately damp grassland with dryads and shrubby willows in the low tundra (Chernyavsky 1969).

Characteristics. Size large: BWt=69–124 g, H&B=110–170 mm, TL=10–20 mm, HF=12–21 mm, EL=8.5–11.5 mm, CbL=29.5–37.8 mm, ZgW=19.4–24.5 mm, MxT=8.6–10.5 mm. Dorsal colouration is variable (ash-grey, buff, fawn, brown), but flanks and belly are grey; demarcation on flanks is distinct (Figure 33). Rump is dark-grey or black. Head is either grey or brown and muzzle is rusty. Spine is distinct and complete (front-to-rump) in ~⅓ of individuals, obscure or absent in the remaining ⅔. Even when absent on the back, the stripe is occasionally bold on the head and nape. Tail and paws are white. Skull is robust and well-ridged, but otherwise as in *novosibiricus*.

Lemmus lemmus kamchaticus new subspecies

Taxonomy. Brown lemmings occupying Kamchatka to the south of the 60th northern parallel were frequently reported under a single name in the past, either *amurensis*, *bungei flavescens* (Fredga et al. 1999), *sibiricus flavescens* (Kuznetsova et al. 1993), *chrysogaster* (Gromov et al. 1963, Gromov & Erbajeva 1995), *obensis (=sibiricus*; Flint et al. 1965), *sibiricus* (Kostenko 1984) or *trimucronatus* (Kostenko 2000). In reality, they belong to both Palaearctic species of brown lemmings, *lemmus* and *nigripes*; the former is represented by 2 lineages, *ognevi* and a nameless lineage (Abramson & Petrova 2018) which is named and described here.

Holotype. Adult male (Zoological Museum of Moscow State University S-101889), skin and skull, Collected by A. Stenchenko on October 12, 1974.

Type locality. The Russian Federation, Kamchatka, Volcano Uzon, Lake Maloe.

Etymology. Named after the Kamchatka Peninsula.

Description of the type. Back is grey-brown to dull-brown, flanks are buffy and belly is grey; the demarcation is fairly distinct (Figure 33). Oral portion of muzzle is rusty. Spinal stripe is distinct on front and nape but blurry posteriorly; black patch is absent on the rump. Feet are greyish-white; tail is silvery-grey with a narrow blackish stripe on the dorsal side; terminal pencil is buff. Dimensions of the type: BWt= 49g, H&B=116

mm, TL=17 mm, HF=18 mm, EL=9 mm, CbL=28.4 mm, ZgW=19.3 mm, MxT=8.3 mm.

Diagnosis and Comparisons. Phylogenetic analysis of *Mt*-DNA haplotypes (Fredga et al. 1999, Abramson & Petrova 2018) retrieved *kamchaticus* as a member of the *amurensis* subspecies group and a close relative to *portenkoi* and *ognevi*. The new subspecies differs from ssp. *portenkoi* in its much smaller size (skull is shorter and narrower and the upper molar row is shorter: CbL=26.3–30.0 mm, ZgW=16.1–18.7 mm, MxT=7.1–8.1 mm, n=14; Chernyavskiy 1984). The new subspecies is categorically larger than ssp. *ognevi* with a bold spinal stripe restricted to the head and nape (frequently reaching the rump in *ognevi*), and a distinct demarcation on the flanks (faint in *ognevi*). Ssp. *amurensis* is approximately the same size as *kamtchaticus* ssp. n. Body mass ($\bar{x}$±*SD*) in 2-month old males is 32.70±1.58 g (n=29) in *kamtchaticus* ssp. n. and 31.07±2.30 g (n=6) in *amurensis* (Kuznetsova et al. 1993). While *amurensis* has bright, usually rusty or rufous pelage, the new subspecies is grey-brown or dull-brown. Furthermore, in *amurensis* the stripe usually spans from front to rump and the black patch is present on the rump in about half of animals (the patch is absent in the new subspecies); the terminal pencil on the tail is all-white in *amurensis* and buff in the new subspecies. See Figure 30 for skull.

Distribution. Known only from Kronotsky Zapovednik, south-eastern Kamchatka.

Lemmus nigripes (True, 1894) – Beringian Brown Lemming

Myodes nigripes True, 1894a:2. Type locality: “St. George’s Island, Alaska”, USA.

Synonyms. *Lemmus obensis chrysogaster* J. A. Allen, 1903; *Lemmus paulus* G. M. Allen, 1914; *Lemmus flavescens* Vinogradov, 1925; *Lemmus xanthotrichus* Vinogradov 1925 [nomen nudum]; Also other synonyms in North America (Musser & Carleton 2005: 988).

Taxonomy. Currently, *nigripes* is classified in *L. trimucronatus* (Richardson, 1852) which is also regarded as the only Nearctic brown lemming (MacDonald & Cook 2009, Pardiñas et al. 2017). The intraspecific genetic diversity in *trimmucronatus* exceeds the one in *lemmus* and the divergence on the Mackenzie River is indicative of 2 cryptic species (Fedorov et al. 2003, Shenbrot & Krasnov 2005). In the past *nigripes* was already recognised as a species in its own right (Davis 1944, Miller & Kellogh 1955, Corbet & Hill 1986) and we reinstate this assertion.

The oldest Palaearctic name for Beringian brown lemmings is *chrysogaster*, which was either considered a species in its own right (Vinogradov 1933, Corbet & Hill 1986, Pavlinov & Lissovsky 2012), a subspecies of a broadly defined *sibiricus* (Hinton 1926a, Gromov & Polyakov 1977), of *obensis* (Ognev 1948, Gromov et al. 1963), of *amurensis* (Musser & Carleton 2005), or a subspecies of *trimucronatus* (Pavlinov & Rossolimo 1998, Shenbrot & Krasnov 2005, Pardiñas et al. 2017). Similarly, *flavescens* was treated as a subspecies of *sibiricus* (Kostenko 1984, Musser & Carleton 1993), *amurensis* (Pavlinov 2006, Pardiñas et al. 2017) or *chrysogaster* (Kuznetzov 1944); *paulus* was understood as a species in its own right (Hinton 1926a), a subspecies of *chrysogaster* (Kuznetzov 1944) or of *sibiricus* (Pavlinov & Rossolimo 1998, Musser & Carleton 1993). These synonyms have only recently begun to be accepted as conspecifics (under *trimucronatus*) (cf. Krasnov & Shenbrot 2005, Pardiñas et al. 2017).

A clear distinction between the Palaearctic *nigripes* and *lemmus* is evident in their karyotypes (see under Characteristics), molecular makeup (Fedorov et al. 2003, Fredga et al. 1999, Abramson & Petrova 2018), and external morphology (Pardiñas et al. 2017). Interspecific cross-breeding trials with various subspecies of *lemmus* (*lemmus, sibiricus, amurensis, portenkoi*, *kamchaticus* ssp. n.) invariably yielded sterile males (Pokrovski et al. 1984, Kuznetsova et al. 1993).

Distribution (Figure 34). The entire range covers 1,106,600 km^2 in Alaska, north-western Canada (west of the Mackenzie River) and north-eastern Russia. Range in Russia (area=156,500 km^2) encompasses the triangle between Chukotka, the lower flow of the Kolyma River, an isolate in southern Kamchatka (*flavescens*), and the north-eastern shore of the Sea of Okhotsk. Principal habitat is shrubby tundra which is widespread along seashores and in river valleys. In the upper reaches of Omolon, lemmings occupy the upper edge of the taiga where they thrive in marshy mires covered with shrubby birch (Chernyavskiy 1984).

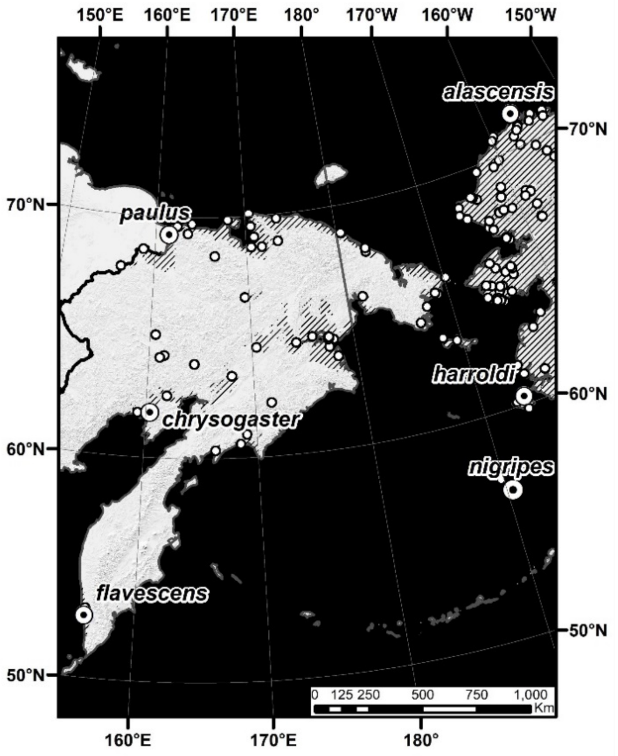


Figure 34: Distribution of the Transberingian brown lemming *Lemmus nigripes*.

Characteristics. External proportions are as in *L. lemmus*, the overall impression however is light and monochromatic (Figure 33). Dimensions: BWt=28–90 g, H&B=101–147 mm, TL=11–19 mm, HF=15–20 mm, EL=6.6–17 mm, CbL=27.0–35.0 mm, ZgW=17.2–24.7 mm, MxT=7.4–9.1 mm. Dorsal fur is grizzled-tawny, darkened between muzzle and shoulders by black hair not found on other parts of the body; the pelage is increasingly fulvous and bright posteriorly from the shoulders. The lower back and rump are yellowish rufous. The muzzle, cheeks, and flanks are orange-ochraceous and a buffy postauricular tuft contrasts the darker dorsal fur. A spinal stripe is rare, evident in ~10% of lemmings; when it is present, it is usually obscure and always restricted to the head or shoulders. The underparts are grey but heavily washed with ochraceous or rusty tints; chin or throat are white in some animals (frequency in Chukotka <5%). Winter fur is longer (length=19.5–24.5 mm on midback, 7–9 mm on the belly) and brighter, and the summer pelage is shorter (length=13.5–15.5 mm and 6–6.5 mm on the back and belly, respectively), darker and without buff tints. Tail is short, club shaped and densely haired, grey with a long (5.2–7.0 mm), light grey or white terminal pencil. Paws are dusky greyish-brown. Dimensions of claws (width×depth of claw on digit III) are 0.84–0.94×1.09–1.56 mm (summer claws) and 0.89–2.61×1.46–2.61 mm (winter claws). Baculum is heavy and robust; the proximal bone (length=2.8 mm) has a broadly expanded base with dorsal and ventral concavities; trident is ossified and the median process is 1.5-times as long as the lateral processes (Anderson 1960). Skull and molars (Figures 30, 31) are as in *L. lemmus*. Karyotype (2n=50) consists of 23 pairs of acrocentric and 1–2 pairs of bi-armed chromosomes (NF$_a$=50, 52). Both heterosomes are large (Rausch & Rausch 1975*,* Chernyavskiy 1984).

Variation and subspecies. Palaearctic populations are usually classified as ssp. *chrysogaster* (Krasnov & Shenbrot 2005) which is possibly synonymous with *alascensis* Merriam, 1900 (Pardiñas et al. 2017); the type locality of *alascensis* is Point Burrow, Alaska.

GENUS: *Myopus* Miller, 1910 – Wood Lemmings

Myopus Miller, 1910:497. Type species is "*Myodes schisticolor* Lilljeborg".

Taxonomy. A monospecific genus which at times in the past was synonymised with *Lemmus* (Miller 1896, Trouessart 1910, Honacki et al. 1982). The sister position of these genera and a monotypy of *Myopus* are robustly supported (Robovský et al. 2008, Steppan & Schenk 2017).

Myopus schisticolor (Lilljeborg, 1844) – Wood Lemming

Myodes schisticolor Lilljeborg, 1844:65. Type locality: "Lille-Hammer [Lillehammer] in Gudbrandsdal [valley in Oppland] in Norway" (p. 70).

Synonyms. *Myopus morulus* Hollister, 1912; *Myopus saianicus* Hinton, 1914; *Myopus thayeri* G. M. Allen, 1914; *Myopus middendorfi* Vinogradov, 1922 [nomen nudum];

Myopus middendorffi Vinogradov, 1922; *Myopus schisticolor vinogradovi* Skalon & Raevskiy, 1940.

Distribution (Figure 35). Taiga belt from Fennoscandia (absent from most of the Kola Penninsula) and European Russia, across Siberia, northern Mongolia, north-eastern China (northern Nei Mongol, Heilongjiang), to the Far East in Russia (including several isolates in western, central and eastern Kamchatka) and the shores of the Seas of Okhotsk and Japan. Sakhalin is the only island occupied by the wood lemming. The entire range covers 7,568,200 km^2. The wood lemming is a species characteristic of the taiga. Main habitat is climax coniferous forests with shrubs and a dense moss stratum; also present in peat bogs and marshy patches in forests (Bobretsov & Lukyanova 2017). Lowland species in the north, but lives in mid- and high elevations in the south; present up to 1,900 m (Altai Mts.) and 2,560 m a.s.l. (Khangay Mts., Mongolia).

Characteristics. Small lemmings of vole-like appearance (Figure 36). Dimensions: BWt=16–59 g, H&B=85–120 mm, TL=11–22 mm, HF=13–16.9 mm, EL=8–12 mm, CbL=23.2–28.2 mm, ZgW=14.0–18.2 mm, MxT=5.1–8.3 mm. Head is rather large and blunt and eyes are small. Pinna is normally developed, larger than in *Lemmus* but still concealed in fur; tragus is absent (Figure 27b). Hands and feet are slender, soles bare with 4 and 6 tubercles, respectively; the 3 posterior plantar pads are the smallest and the lateral metatarsal is particularly reduced in some individuals. The claws are the same size throughout the year; the nail on the front thumb is large (Figure 25b), like in *Lemmus*.

Fur is soft and dense, longer dorsally (9.5–13 mm) than ventrally (5.5–8 mm). Pelage is dark-grey (slate) and the majority of animals have rusty-brown rumps (type b in Figure 37). A rusty patch is usually (~90%) restricted to the rump; it is rarely absent or expanded across the back. The intensity also varies individually and seasonally; the patch is more prominent in summer and fades in winter (Gromov & Erbajeva 1995). Tail is densely furred, either uniformly dark or bi-coloured (black above, whitish below) with a terminal pencil (length=2.5–6 mm). Females have 8 nipples. Baculum as in *Lemmus*; the proximal stalk (length=1.99 mm) has a widely expanded base (width=0.99 mm). Distal digits are of approximately the same length; the central digit is less than half the length of the proximal bone (Artimo 1969). The skull is similar to that of *Lemmus* but the dorsal profile is more convex, ridges less prominent, rostrum shorter, brain-case relatively longer, nasals narrower and interorbital region broader (Figure 38). Teeth are as in *Lemmus*, apart from a shortened and wider M^3 (Figure 39). Karyotype (2n=32) of mostly bi-armed chromosomes is found throughout the range; some

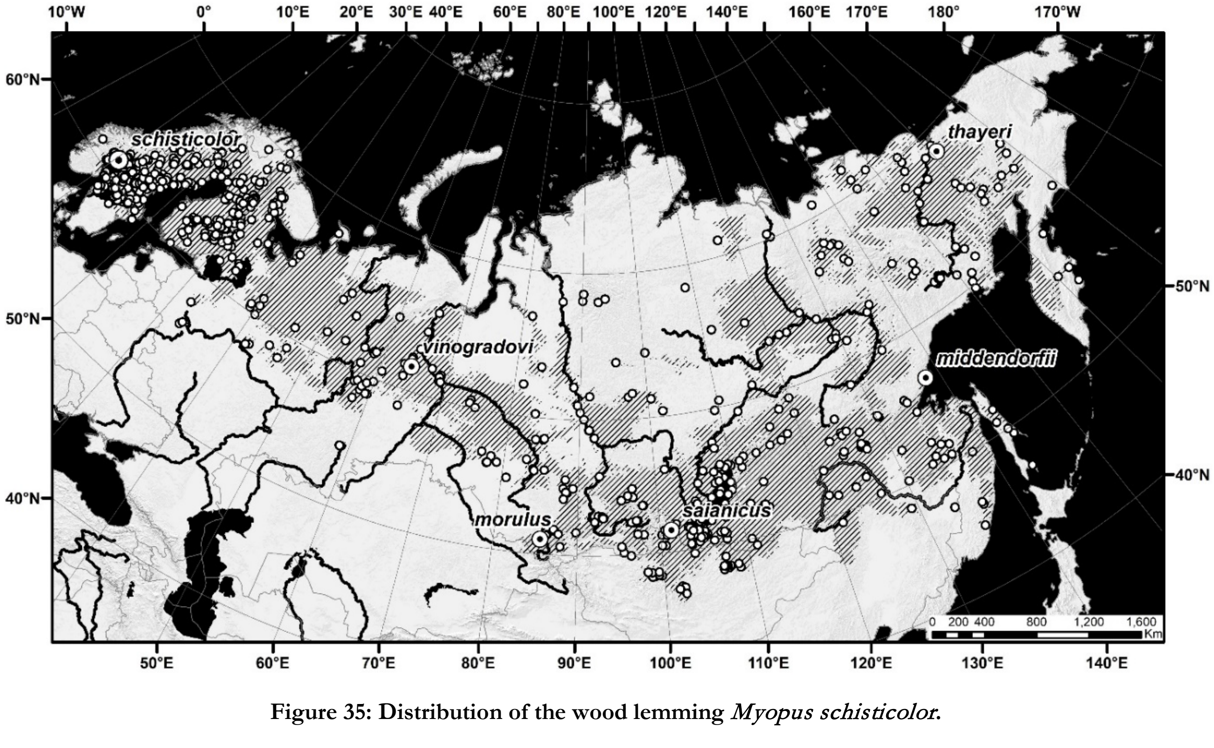


Figure 35: Distribution of the wood lemming *Myopus schisticolor*.

Figure 36: Wood lemmings (*Myopus schisticolor*) from Norway. Photo courtesy Aina Bye (left inset) and Roar Solheim.

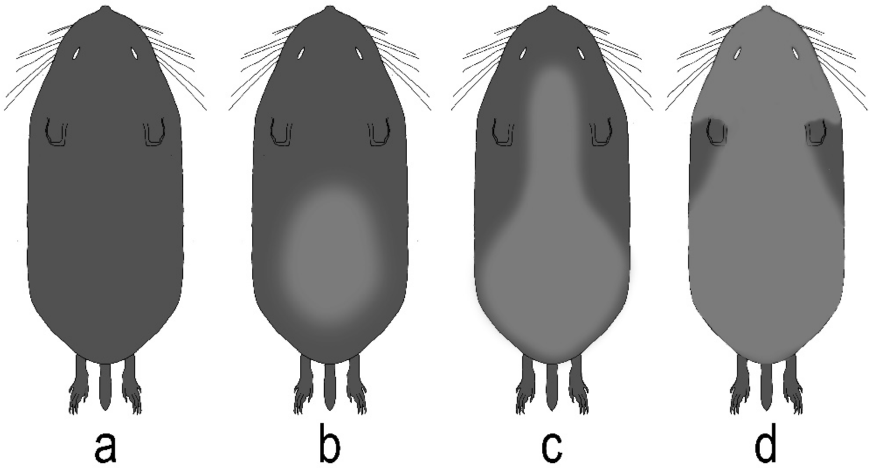


Figure 37: Schematic presentation of variation in size and shape of the rusty spot (light grey) in wood lemmings *Myopus schisticolor* from (a) Sakha, (b) Finland, (c) Altai Mts., and (d) northern Mongolia.

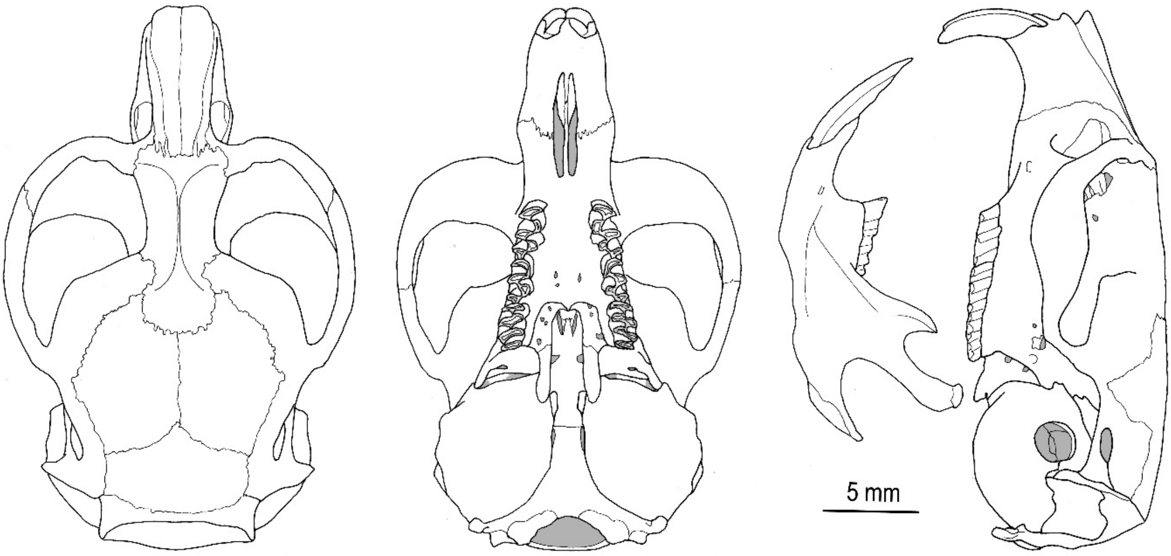


Figure 38: Skull and mandible in *Myopus schisticolor* from Ulus Verkhojanskiy, estuary of the Tuostah River, Sakha Republic, Russian Federation.

populations display 2n=32–34 (Kozlovsky 1974, western populations have 2n=31, and certain eastern Kozlovskij 1986, Stenseth & Ims 1993). Female heterosomes are either XX or XY (Fredga 1988).

Variation and subspecies. Five subspecies (the nominal, *morulus, thayeri, saianicus, vinogradovi*), recognised by the majority of authors (Ognev 1950, Gromov & Polyakov 1977), are loosely defined by colour details with no proof of discontinuity (Gromov & Erbajeva 1995). Size seems to be invariant across the range and no differences were reported in dentition or skull shape (Kratochvíl et al. 1979). Phylogeographic assessment based on *Cytb* gene retrieved 2 lineages separated by only 7 mutation steps (nucleotide divergence=0.9%). The south-eastern lineage is known from a relatively small area in Transbaikal (=Chita) and upper Amur (both in Russia) while the Northern lineage occupies the vast majority of the species' range and encompasses all recognised subspecies. The Northern lineage is further structured into 3 sub-lineages: the Western, Central and Eastern (Fedorov et al. 2008).

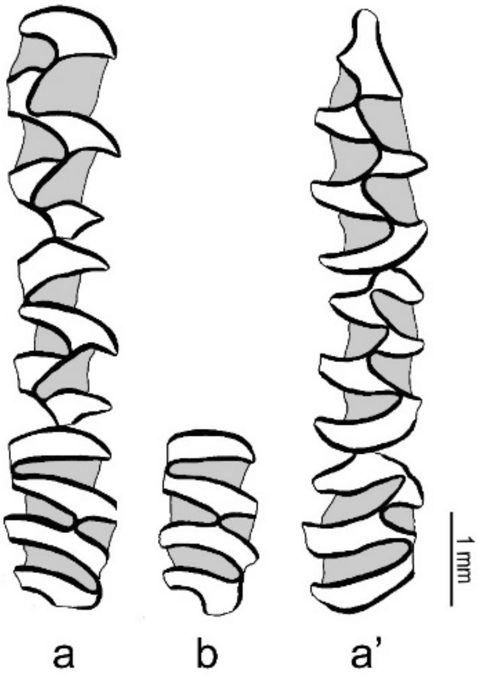


Figure 39: Molar grinding pattern in *Myopus schisticolor*. Shown are upper (a) and lower (a') molar row, respectively, and isolated M3 (b). Origin of vouchers (both from Russian Federation): a–Altai Mts.; b–Magadan Oblast.

TRIBE:
Clethrionomyini Hooper & Hart, 1962

Taxonomy. One of the major tribes of Arvicolinae, characterised by the structure of the posterior palate. Its taxonomic scope remained relatively stable over time. Gromov & Polyakov (1977) also included *Dinaromys* (now in Arvicolini) in this tribe and some authors classified Clethrionomyini as a subtribe of Arvicolini (Pavlinov & Rossolimo 1987) or Prometheomyini (Pavlinov et al. 1995, Pavlinov & Rossolimo 1998). Kretzoi (1969a) proposed Myodini as a replacement name for Clethrionomyini but this violates Article 40.1. of the Code and is considered invalid.

The tribe consists of two major phylogenetic lineages (Tang et al. 2018, Steppan & Schenk 2017) ranked here as subtribes of Clethrionomyina and Eothenomyina new substribe.

Distribution. Temperate, boreal and Arctic habitats of the Holarctic region. *Anteliomys* and *Eothenomys* occupy subtropical and marginally tropical mountain areas in the Palaearctic-Oriental transitional zone, reaching Taiwan and the northernmost parts of Myanmar and Indochina. Several species have extensive Palaearctic ranges and *Clethrionomys rutilus* is trans-Beringian in its distribution. Small-range endemics occupy the eastern and southern margins of the range in west-Pacific islands and Korea (*Craseomys*), Sichuan and Hengduan Mts. in China and Myanmar (*Anteliomys* and *Eothenomys)*, the Himalayas and sporadically Siberia (*Alticola*).

Clethrionomyini are more closely tied to forest environments than the majority of remaining arvicolines and avoid flat short-grass steppes. Typical habitats include grassland and clearings with a dense, tall herbal layer, successional stages towards the forest, shrubs, forest edge, closed-canopy forests (mesic evergreen, deciduous, mixed and coniferous stands), and rocky situations. In the south, these voles are typically found in cooler and mesic habitat islands at high altitudes.

Characteristics. The posterior palate terminates as a simple shelf and the postero-lateral pits open directly to choanae (Figures 9a, 10d). Molars are rooted or rootless and both conditions may occur in the same genus (*Craseomys*) or even the same species (*Craseomys rufocanus*). Enamel is thin, salient angles are rounded and the cement either partly fills re-entrant angles or is absent. Differentiation of the enamel layer is either negative (*Clethrionomys, Craseomys*) or positive (*Alticola, Eothenomys, Aschizomys*). The enamel pattern (schmelzmuster) always contains at least some lamellar enamel but the convex (leading) edges of the triangles are usually of a tangential type (Koenigswald 1980). The distal baculum is ossified but detailed information is currently unknown for several groups; females have 4, 6, or 8 nipples. Romanenko et al. (2018) detected intrachromosomal changes (mainly pericentric inversions) in two evolutionary conserved chromosome segments (syntenies), which are synapomorphic for Clethrionomyini (Myodini in their nomenclature). Heterosomes form synaptonemal complexes during pachytene in both sexes (Borodin et al. 1995).

Key to genera

1a) 2 pairs of nipples 2
1b) 3–4 pairs of nipples (2–3 pairs in *Craseomys smithii* of Japan) 4
2a) Opposite dental fields alternate ....*Caryomys*
2b) Opposite dental fields (particularly on M^2 and M_1–M_3) widely confluent 3
3a) M^1 with a postero-lingual salient angle (LS4); 4 inner salient angles ....*Eothenomys*

3b) M^1 lacks a postero-lingual salient angle (LS4); 3 inner salient angles ....*Anteliomys*

4a) Mid-back usually grey (brown in *roylei* and *montosus*); molars tend to be compressed laterally with little or no cement in re-entrant angles; M^3 with T2 reduced and widely confluent with AL (except in *A. montosus*); positive differentiation of enamel ....*Alticola*

4b) Mid-back rusty or brown (not grey); molars normal, not compressed laterally with abundant cement in re-entrant angles; M^3 with T2 of normal size and isolated from AL; negative differentiation of enamel...................5

5a) Molars rootles ....*Craseomys (Phaulomys)*

5b) Molars rooted in adults 6

6a) Larger on average; development of roots postponed into adult age; postorbital processes and temporal ridges usually prominent; salient angles more pointed ....*Craseomys*

6b) Smaller on average; roots develop earlier; postorbital processes and temporal ridges normally ill-defined; salient angles more rounded ....*Clethrionomys*

SUBTRIBE: Clethrionomyina Hooper & Hart, 1962

Clethrionomyini Hooper & Hart, 1962:64. Type genus is *Clethrionomys* Tilesius.

Synonyms. Myodini Kretzoi, 1969; Alticoli Gromov, 1972.

Distribution. Holarctic subtribe; in China only slightly transgresses the Huang He River and occurs in sympatry with Eothenomyina. All Nearctic Clethrionomyini are from this subtribe.

Characteristics. See under Eothenomyina. Karyotype: 2n=56. Pelage is brown (frequently shaded rusty) or grey. Females have 8 nipples; only *Craseomys smithii* has 4–6 nipples. Skull is lightly built with weak temporal ridges, lambdoidal crest and postorbital (squamosal) process; interorbital region is usually constricted. Front surface of upper incisors is smooth; molars are rootless or develop roots with age. Dental fields of opposing triangles usually alternate; M^1–M^2 without additional postero-lingual salient angle LS4 (T5); M^3 with 3–4 lingual salient angles.

GENUS: *Clethrionomys* Tilesius, 1850 – Red-backed Voles

Clethrionomys Tilesius, 1850:28. Type species by subsequent designation: *Mus rutilus* Pallas (Palmer 1928:87).

Synonyms. *Evotomys* Coues, 1874; *Glareomys* Razorenova, 1952.

Taxonomy and Nomenclature. A Holarctic genus of five species. In the past *Clethrionomys* also included species which are now in *Craseomys* and *Caryomys*. The distinction between *Clethrionomys* and *Craseomys* was found in the karyotype (Modi & Gamperl 1989, Sokolov et al. 1990), acoustics (Rutovskaya 2019a), sperm morphology (Dimitriev et al. 1991), allozymes and nucleotide sequences. In phylogenetic trees the *Clethrionomys* + *Craseomys* clade emerged paraphyletic with respect to *Alticola* (Tang et al. 2018). The monophyly of *Clethrionomys* is therefore possible only with the exclusion of *Craseomys*. The reconstructions of phylogenetic relationships within *Clethrionomys* are often problematic due to recent radiations and frequent episodes of hybridisation and gene introgression (cf. Kohli et al. 2014). Most notably, in the recent past *Alticola macrotis* was classified in *Myodes* (=*Clethrionomys*) on the basis of alien *Mt*-DNA (Lebedev et al. 2007, Pardiñas et al. 2017).

Two generic names were used for red-backed voles throughout the 20th century, firstly *Evotomys* (Miller 1900) and afterwards *Clethrionomys* (Palmer 1928). Kretzoi (1964) claimed the priority of *Myodes* over *Clethrionomys* which was followed in Carleton et al. (2014), Musser & Carleton (2005), Pavlinov (2006), and Pardiñas et al. (2017), but opposed in Corbet (1978) and Tesakov et al. (2010). The source of disagreement is the fixation of the type species for *Myodes*. As argued by Kryštufek et al. (2020), Coues' (1877) act of fixing *Mus lemmus* as the type species of *Myodes* fulfils the stipulations of the Code. *Myodes* is therefore antedated by *Lemmus* Link, 1795. Lataste's (1883a) fixation of *Mus rutilus* as the type of *Myodes* is predated by Coues (1877) and therefore invalid for that reason. The genus group name *Myodes* is therefore not available for red-backed voles and the oldest available name is *Clethrionomys*.

Geographical Range. Widespread and abundant in temperate deciduous, mixed and coniferous forests, and in boreal habitats (taiga and forest tundra) throughout the Holarctic region.

Characteristics. Small to medium sized voles of slender body form (Figure 40). Tail is moderately long (TL/H&B=0.33–0.60), rather densely clothed with hair and a distinct terminal pencil (Figure 41). Hands and feet are small, each with five digits armed with small but sharp claws. Digits are long, except for the much-reduced thumb, which still has a flat nail. Palms and soles are naked with 5 and 6 pads respectively (Figure 42). In contrast to *Microtus* voles, the snout is more pointed, the eyes are larger and the semi-circular ears overtop the fur. Hair is dense, softer in winter and coarser in summer. Colour is variable but upper flanks usually have distinct rusty mantle; underside is grey or silver; hair bases are slate throughout. Females have 8 mammae. The baculum is of characteristic trident shape with a basal shaft and three ossified digital processes at the tip.

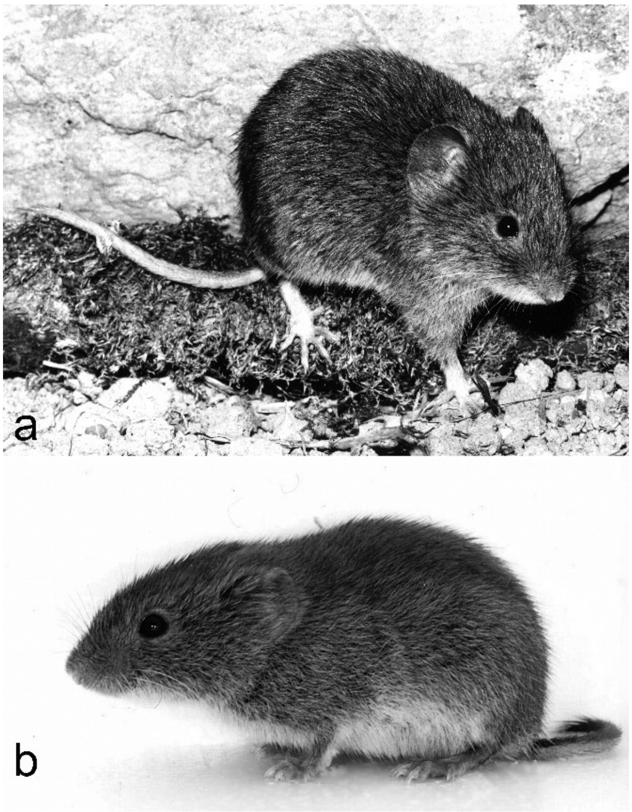


Figure 40: Red-backed voles: a–*Clethrionomys glareolus* (Czech Republic); b–*C. rutilus* (Hokkaido, Japan). Photo courtesy Miloš Anděra (a) and Masahiro A. Iwasa (b).

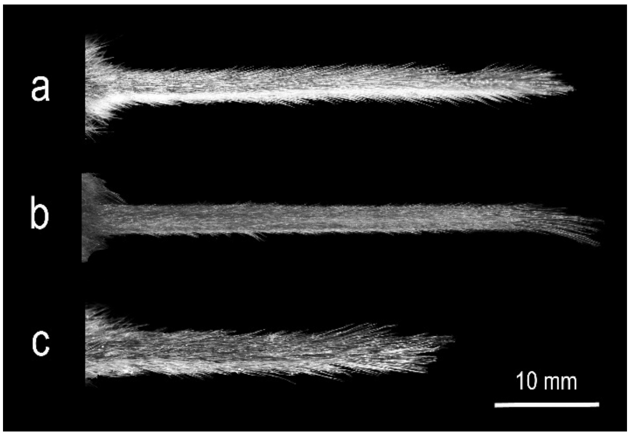


Figure 41: Tail in red-backed voles (dorsal view): a–*Clethrionomys glareolus* (Leninogorsk District, Tatarstan, Russian Federation); b–*C. centralis* (Zailiyskiy Alatau, Kazakhstan); c–*C. rutilus* (Atka, Magadan, Russian Federation). Photo: B. Kryštufek.

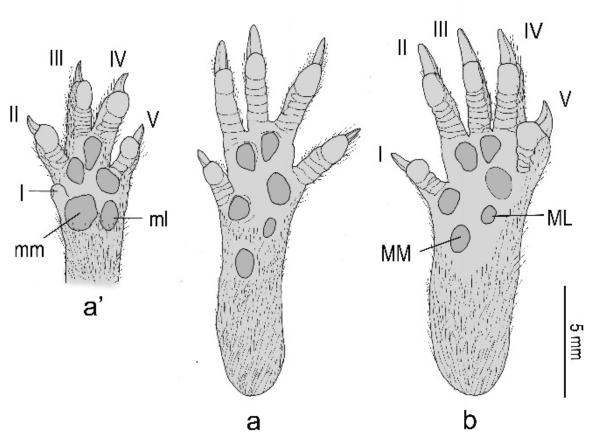


Figure 42: Left palm (a') and sole (a,b) in *Clethrionomys glareolus* (a–Lendava, Slovenia) and *C. rutilus* (b–Lake Grand, Magadan, Russian Federation). Digits are indicated by Roman numbers (thumb=I). Metacarpal and metatarsal pads are specified by lower and upper case letters, respectively: mm/MM–medial pad, ml/ML–lateral pad.

The skull is lightly built without prominent ridges; zygomatic arches are slender and moderately expanded, rostrum is rather weak. Interorbital region is wide and flat, postorbital processes are small, and brain-case is broadly oval. Dorsal profile is smooth and slightly convex. Bullae are of circular outline and fairly large. Bony palate terminates in a simple transverse bony shelf; pterygoid fossa is shallow. Mandible is slender and weak (Figure 43). The incisors are not as robust as in *Microtus* and the molars are comparatively smaller. Lower incisor root is short, extending to the labial side of molar roots and reaching the base of the condylar process; there is

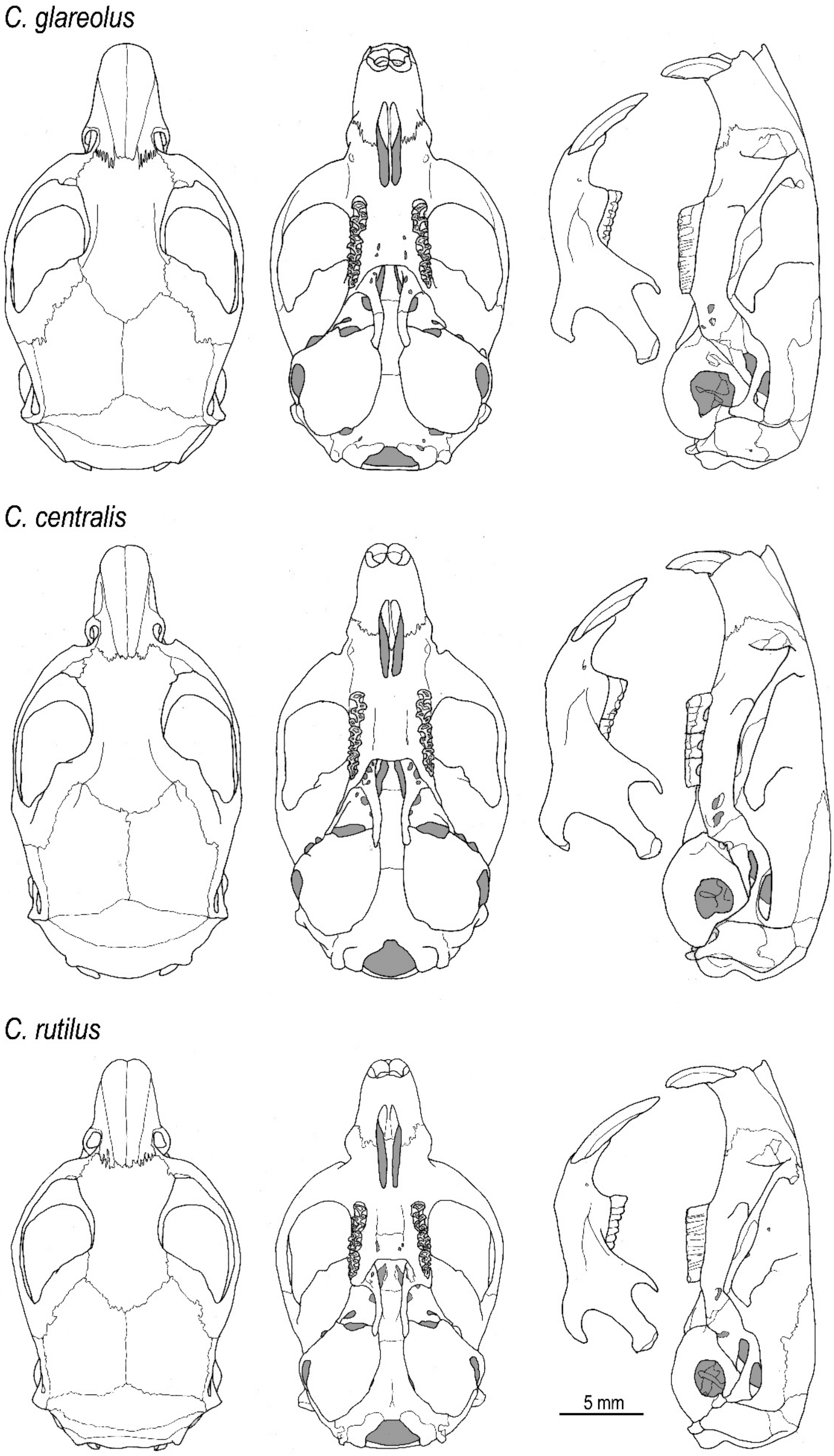


Figure 43: Skull in red-backed voles: top–*Clethrionomys glareolus* (Garmish Partenkirchen, Bavaria, Germany); middle–*C. centralis* (Aksunskiy, Arashan, Kyrgyzstan); bottom–*C. rutilus* (Atka, Magadan, Russian Federation).

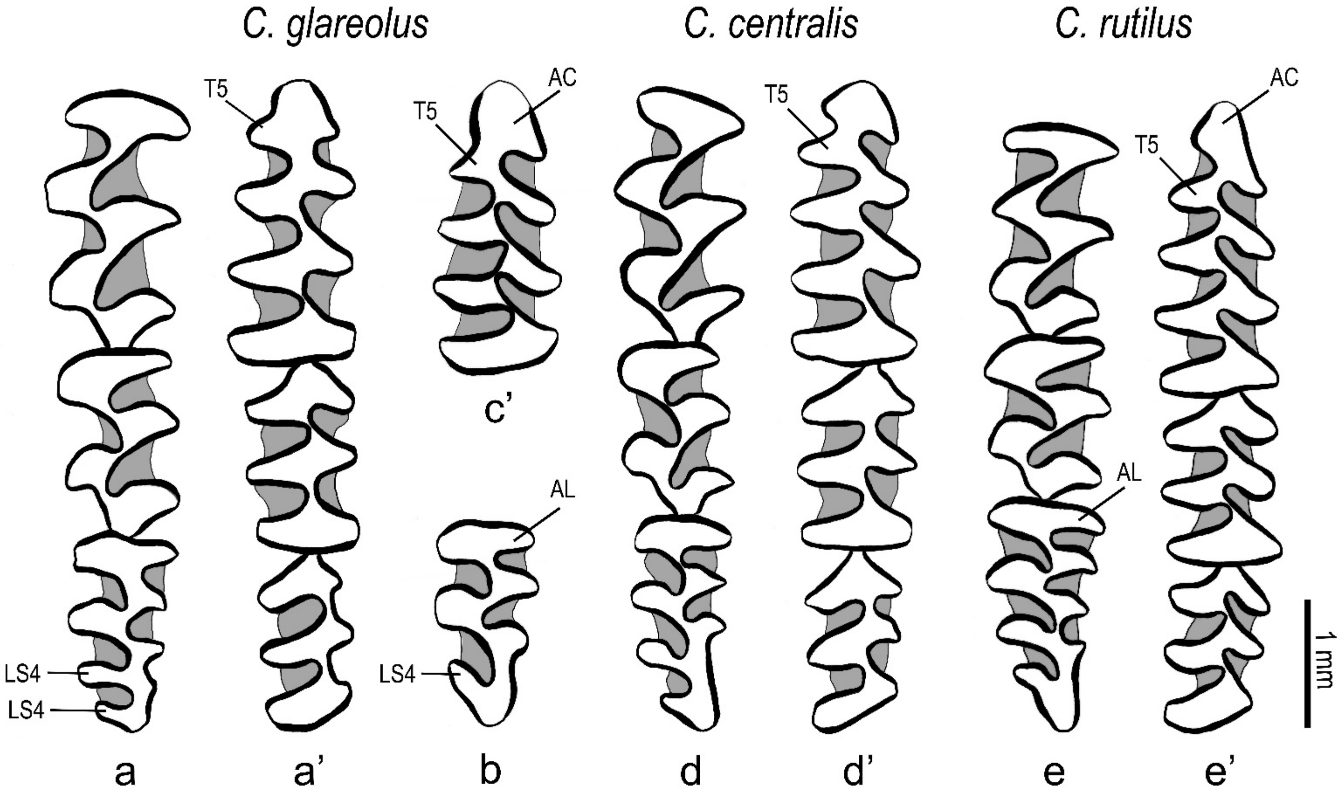


Figure 44: Molar pattern in red-backed voles. *Clethrionomys glareolus*: upper (a) and lower row (a'–Camigliatello Silano, Calabria, Italy); isolated M^3 (b; Foresta Umbra, Monte Gargano, Italy); isolated M1 (c'–Pirin Mts., Bulgaria). *C. centralis*: upper (d) and lower row (d'–Lake Almatinskoe Lake, Kazakhstan). *C. rutilus*: upper (e) and lower row (e'–Pektu-san, North Korea).

no bulge at this point. Molars are rootless in young animals and grow from a pulp. Afterwards 2 roots develop on each molar (rhizodont condition); in free-living *C. glareolus* this happens at 8–18 weeks of age ($\bar{x}$≈3.5 months; Mazák 1963). Enamel is thin (0.06–0.09 mm thick in *glareolus*; Koenigswald 1980) and negatively differentiated; the schmelzmuster contains lamellar enamel in the leading edges and tangential enamel in the trailing edges (Koenigswald 1980). Re-entrant angles are partly filled by cement and salient angles are rounded. The upper molars have 4 (M^1) and 3 (M^2) alternating triangles, respectively. The variation in length and complexity of the posterior lobe on M^3 depends on the number of lingual salient angles which are either 3 or 4; M^3 is relatively longer in *glareoleus* than in *rutilus* and its anterior loop is less squeezed. The M$_1$ has 4 alternating triangles; T5 is either closed or broadly confluent with the anterior cup. The M$_2$–M$_3$ have 3 salient angles on each side; triangles tend to fuse into transverse loops (Figure 44). Karyotype is conservative and stable among species: 2n=NF$_a$=56.

Key to species

1a) Root of upper incisor longer, nearly reaching the anterior root of M^1; back usually brownish without rusty tint .... *centralis*
1b) Root of upper incisor shorter, terminates well before reaching the anterior root of M^1; back usually distinctly reddish 2
2a) TL/H&B≈0.33; tail is densely clothed; terminal pencil longer (Figure 41c) .... *rutilus**
2b) TL/H&B≈0.5; tail is moderately clothed; terminal pencil shorter (Figure 41a) ....*glareolus**

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* *C. rutilus* has shorter molars than sympatric *C. glareolus* in the Urals and Western Siberia; length of M^1=1.48–1.85 mm in *rutilus* and 1.80–2.25 mm in *glareolus*; range for length of M^2 is 1.10–1.35 mm and 1.35–1.65 mm, respectively (Borodin et al. 2005).

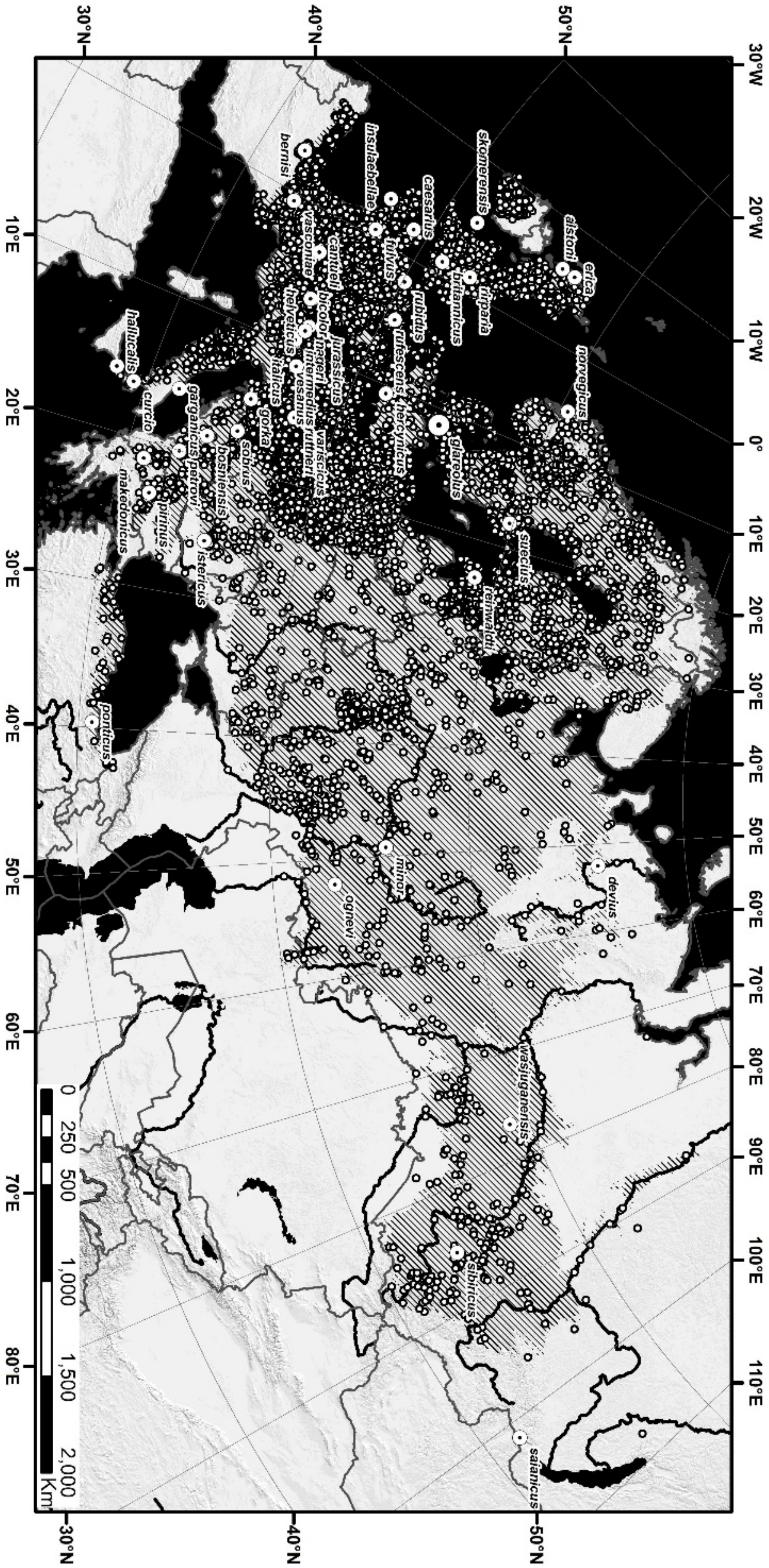


Figure 45: Distributional range of the bank vole *Clethrionomys glareolus*.

Clethrionomys glareolus (Schreber, 1780) – Bank Vole

Mus glareolus Schreber, 1780:680 + Plate 190 B. Type locality: "Island Laland, on […] the coast of Ostsee", currently the Island of Lolland, Denmark (Miller 1912a:632).

Synonyms. *Mus rutilus minor* Kerr, 1792 [nomen dubium]; *Lemmus arvalis* É. Geoffroy Saint-Hilaire, 1803 [unavailable name]; *Arvicola fulvus* Millet, 1828 [not *Lemmus fulvus* Geoffroy, 1803]; *Hypudacus* [sic] *hercynicus* Mehlis, 1831; *Arvícola ripària* Yarrell, 1832; *Lemmus rubidus* Baillon, 1834; *Arvicola rufescens* Sélys-Longchamps, 1836; *Hyp[udæus] Nageri* Schinz, 1845; *Myodes bicolor* Fatio, 1862; *Evotomys norvegicus* Miller, 1900; *Evotomys vasconiæ* Miller, 1900; *Evotomys hercynicus helveticus* Miller, 1900; *Evotomys hercynicus suecicus* Miller, 1900; *Evotomys hercynicus brittanicus* Miller, 1900; *Evotomys skomerensis* Barrett-Hamilton, 1903; *Evotomys ponticus* Thomas, 1906; *Evotomys nageri hallucalis* Thomas, 1906; *Evotomys cæsarius* Miller, 1908; *Evotomys glareolus istericus* Miller, 1909; *Evotomys glareolus saianicus* Thomas, 1911; *Evotomys erica* Barrett-Hamilton & Hinton, 1913; *Evotomys alstoni* Barrett-Hamilton & Hinton, 1913; *Evotomys glareolus reinwaldti* Hinton, 1921; *Evotomys glareolus jurassicus* Burg, 1924; *Evotomys glareolus intermedius* Burg, 1924; *Evotomys glareolus sobrus* Montagu, 1923; *Evotomys gorka* Montagu, 1923; *Evotomys glareolus italicus* Dal Piaz, 1924; *Clethrionomys glareolus pirenaica* Cabrera, 1924 [unavailable name]; *Evotomys nageri vesanus* Hinton, 1926; *Evotomys glareolus ognevi* Serebrennikov, 1927; *Evotomys glareolus sibiricus* Egorin, 1936; *Evotomys glareolus wasjuganensis* Egorin, 1939; *Clethrionomys glareolus insulæbellae* Heim de Balsac, 1940; *Clethrionomys glareolus pirinus* Wolf, 1940; *Clethrionomys glareolus* natio *bosnensis* V. Martino, 1945 [published as natio; valid as *bosnensis* Dulić & Tortić, 1960]; *Clethrionomys glareolus* natio *petrovi* V. Martino, 1945 [published as natio; valid as *petrovi* Dulić & Tortić, 1960]; *Clethrionomys glareolus devius* Stroganov & Tureva, 1948; *Clethrionomys glareolus tomensis* Heptner, 1948 [substitute name for *sibiricus* Egorin, 1939]; *Clethrionomys glareolus variscicus* Wettstein, 1954; *Clethrionomys glareolus garganicus* Hagen, 1958; *Clethrionomys glareolus curcio* Lehmann, 1961; *Clethrionomys glareolus makedonicus* Felten & Storch, 1965; *Clethrionomys glareolus cantueli* Saint Girons, 1969; *Clethrionomys glareolus bernisi* Rey, 1972; *C[lethrionomys] g[lareolus] angulatus* Petrov, 1992 [nomen nudum].

Taxonomy. Earlier authors divided bank voles into up to 8 species (e.g. Hinton 1926a). Italian bank voles are the most distinct. Král et al. (1971) reported sterile F2 hybrids between the West-European bank voles and topotypes of *garganicus* from southern Italy and more recently Gippoliti (2013) elevated the phylogeographic lineage from Calabria (Colangelo et al. 2012, Filipi et al. 2015) to a species in its own right (*hallucalis*).

Limited episodes of past and present hybridisation with *rutilus* have been documented in the zone of sympatry and all voles with the alien *Mt*-genome were *glareolus*. Though the current extent of hybridisation is very low, on average 27% of *glareolus* in European Russia display *rutilus* mitotype; in some regions (e.g. Kola) all *glareolus* have *rutilus Mt*-DNA (Potapov et al. 2007, Melnikova et al. 2012). Introgression of nuclear genes was not detected (Boratińsky et al. 2014). Captive crossbreeding between *glareolus* and *centralis* was only occasionally successful (Zimmermann 1965, Bashenina 1981). Viable F1 hybrid offspring were produced in breeding trials between *glareolus* and the Nearctic *gapperi* (Grant 1974).

Distribution (Figure 45). Range extends from the Atlantic Coast to Yenisey and Lake Baikal, and from beyond the Arctic Circle as far south as ~40–50th northern parallel. The entire range covers 8,956,090 km². In the south, the bank vole is frequently restricted to the mountains, specifically to the Cantabrian Mts. and the Pyrenees in northern Spain, the Apennines (Italy), the Balkan Mountains, the Pontic Mts. in northern Anatolia, and the Altai and Sayan Mts. in Central Asia. In the lowlands of European Russia, the range follows the forest-steppe zone along the lower reaches of the Don River and the middle reaches of the Volga and Ural Rivers (Shenbrot & Krasnov 2005). Altitudinal range is from sea level up to the timberline), reaching 1,300 m in the southern Urals, 1,650 m in the Carpathians, 1,900 m in the Altai, 2,375 m in the Balkans, 2,020 m in the Lesser Caucasus (Georgia), 2,100 m in Anatolia, 2,570 m in the Pyrenees, and 2,700 m in the Alps. Bank voles are common on the islands off the Baltic and Atlantic coasts. In Ireland, where they have been known since 1964, it is possible that voles were accidentally introduced from Germany in the 1920s. Spreading at a rate of 2–4.5 km/year in the 1970s, it is anticipated that they will occupy all of Ireland in due course. After 1975, bank voles colonised Ushant Island, Brittany, France (Lorvelec et al. 2019). Deciduous, mixed and coniferous forests are the main habitat and the dense cover of tall herbaceous plants is preferred (Mazurkiewicz 1994). Occasionally bank voles are found in crop fields, rocky situations, in shrubs and on various successional stages in forest clearings.

Characteristics. Dimensions: BWt=21–39 g, H&B=81–123 mm, TL=37–70 mm, HF=14–21 mm, EL=11.4–15 mm, CbL=21.7–26.2 mm, ZgW=12.0–14.9 mm, MxT=4.8–6.1 mm. The tail is ~½ the length of the head and body, moderately haired, rather distinctly bi-coloured (Figure 40a). Dorsum is reddish varying from yellowish wood-brown and cinnamon to dull reddish-brown; flanks are grey. Underside is light grey with a variable buff wash. Baculum is 3.45–4.25 mm long and 0.85–1.3 mm wide across the base (specimens from Finland; Artimo 1964). Sperm head is shorter (length=6.4–7.2 μm) than in *C. rutilus* and thickened at the base (Smirnov et al. 2021). Skull shows no peculiarities (Figure 43); the posterior margin of the hard palate is continuous. M^3 has 3–4 lingual salient angles; the two variants are referred to as simplex and complex morphotypes, respectively. Karyotype: 2n=56, NF=60, NF_a=56, X is large acrocentric, Y is small acrocentric or bi-armed (Zima & Král 1984, Yoshida et al. 1989, Sokolov et al. 1990).

Variation and subspecies. A number of subspecific names are available (Figure 45) with little consensus having been reached on the actual number of valid subspecies. Niethammer & Krapp (1982) list 26 subspecies for western and central Europe but this number is usually lower in other compilations, e.g Gromov & Polyakov (1977) and Bashenina (1981) recognised 13 and 10 subspecies, respectively, for the entire range. Corbet (1978:99) stressed that “in the absence of any descriptive revision of subspecific variation covering the entire range of the species most of the [...] names have little meaning.”

Phenetic interpopulation variation is evident in colour, size, body proportions, and the frequency of molar morphotypes. Some marginal isolates are morphologically quite unique. Colour displays no large-scale trend (Petrusewicz 1983). Size ($\bar{x}$ CbL) ranges from <23 mm (e.g. 22.4 mm in Kemerovsk, Russia; 22.8 mm in England; 22.9 mm in the Altai), to >25 mm (e.g. 25.1 mm in Komi, Russia; 25.2 mm in the Swiss Alps and the Pyrenees, respectively; 25.7 mm on Monte Gargano, Italy). Populations occupying the central and eastern portions of the range are usually small to medium ($\bar{x}$ CbL<23.5 mm). Large bank voles live in southern and western mountainous regions, on islands off the coast of Britain, and in northern European Russia. In Europe the mountain populations are larger than those in the lowlands (Petrusewicz 1983). Demographic strategies explain geographic variation in body size better than ecogeographic rules (Hansson 1985). Relative length of the tail (TL/H&B) varies, e.g. in Europe the population mean is 0.42–0.60, depending on population (Niethammer & Krapp 1982). Growth of tail relative to head and body is isometric in lowland populations and allometric at high altitudes (Claude 1967). Regional differences were also reported in litter size, weight of neonates, social behaviour, activity levels, diet, and length of intestine. Populations from southern Scandinavia are more similar to Central-European populations than to those in north-Scandinavia and the variation likely reflects differences in demographic strategies (Hansson 1985).

The incidence of a complex morph of M^3 is from zero to one hundred percent; 48–85% of individuals have a complex pattern (median=61%) in the majority of European populations. In Central Europe, populations from high elevations display a higher incidence (>80%) of complex M^3 than those from the lowlands where <60% is normal (Bauchau & Chaline 1987). The opposite holds true in Siberia where populations from the Altai and Sayan Mts. (in addition to those from the Yenisey basin) have a high proportion of simplex morphotype, but this may relate to diet (Okulova & Andreeva 2008). Furthermore, a significant shift in morphotype frequency may occur in the same population within a few decades (Corbet 1975).

The only notable chromosomal polymorphism associates with Y chromosome. This heterosome is acrocentric throughout the majority of the species’ range, and is bi-armed in southern Italy and the Balkans; the transition between the acrocentric and bi-armed condition is gradual in the Balkans (Mitsainas et al. 2008).

The phylogeographic pattern suggests a complex evolutionary history of survival in multiple glacial refugia followed by a secondary admixture of allopatrically evolved lineages. Approximately 7 *Mt*-lineages have been recovered thus far: (i) West-European (France, Britain, the Alps, Germany and the western Balkans), (ii) East-European (from S Fennoscandia, eastern Germany and the Carpathian basin eastward to southern Siberia), (iii) Balkan (eastern Balkans and Asia Minor), (iv) south-west European (Italy and northern Spain), and (v) Basque lineage (Basque country and the Atlantic Pyrenees, both in France). The oldest lineages are endemic to traditional Mediterranean refugia in Italy, the Balkans, and particularly northern Spain (Deffontaine et al. 2009, Colangelo et al. 2012). Populations in different parts of Europe, however, have admixed origins from the Mediterranean and the Carpathian sources (Horníková et al. 2021). Bank voles from northern Spain are recognisably distinct in morphology (Rey 1972).

Clethrionomys rutilus (Pallas, 1779) – Siberian Red-backed Vole

Mus rutilus Pallas, 1779:246. Type locality: "[…] in omni Sibiria transobenſi, […] ad ipſum Obenſem captum […] In Dauriæ ſylvis […] ab Lenam […]a Iacutis […] in Kamtſchatka […]", i.e. [the entire Siberia east of the Ob' River, Transbaikalia, on the River Lena, in Yakutia (Saha), Kamtchatka]. Type locality was subsequently restricted to "Zaobskaya kotlovina" [middle reaches of the Ob' River] (Ognev 1950: 131) which was précised as "Kolpashevsiy r-n [Raion]" (Pavlinov & Rossolimo 1987: 182), Tomsk Oblast, Russian Federation.

Synonyms. *Arvicola (Hypudæus) amurensis* Schrenck, 1859; *Arvicola (Hypudæus) russatus* Radde, 1861; *Evotomys jochelsoni* J. A. Allen, 1903; *Evotomys mikado* Thomas, 1905; *Microtus mollessonae* Kashchenko, 1910; *A[rvicola] putaceus* Gillot, 1910 [nomen nudum]; *Evotomys baikalensis* Ognev, 1923; *Evotomys laticeps* Ognev, 1923; *Evotomys parvidens* Ognev, 1923; *Evotomys otus* Turov, 1924; *Evotomys rutilus jacutensis* Vinogradov, 1927; *Clethrionomys rutilus rossicus* Dukelskaya, 1928; *Evotomys rutilus volgensis* Kaplanov & Raievsky, 1928; *Clethrionomys yesomontanus* Kishida, 1931 [nomen nudum]; *E[votomys] r[utilus] uralensis* Vinogradov, 1933 [nomen nudum]; *E[votomys] r[utilus] tugarinovi* Vinogradov, 1933 [nomen nudum]; *E[votomys] r[utilus] hintoni* Vinogradov, 1933 [nomen nudum]; *Evotomys rutilus vinogradovi* Naumov, 1934; *Evotomys rutilus salairicus* Egorin, 1936; *Evotomys rutilus uralensis* Kolyushev, 1936 [new name]; *Evotomys rutilus lenaensis* Kolyushev, 1936; *Evotomys rutilus hintoni* Zolotarev, 1936 [new name]; *Evotomys rutilus narymensis* Egorin, 1939; *Clethrionomys rutilus lategriseus* Argyropulo & Afanasiev, 1939; *Clethrionomys rjabovi* Belyaeva, 1953; *Clethrionomys rutilus tundrensis* Bolshakov & Shwarz, 1965; *Cl[ethrionomys] r[utilus] finmarchius* Siivonen, 1967. Also other synonyms in North America (Hill 1981).

Taxonomy. Taxonomic and geographic scope of *rutilus* has remained relatively stable since the late 19th century. The most divergent taxonomy was by Hinton (1926a) who recognised 8 species in addition to *rutilus* (*amurensis, baikalensis, jochelsoni, laticeps, mikado, otus, parvidens,* and *wosnessenskii*). Coues (1877) used *rutilus* for the North American representatives and Miller (1900) applied this name to both the European and Asiatic populations.

Clethrionomys rutilus is broadly sympatric with *glareolus* and parapatric with the Nearctic *gapperi*, and hybridise with both. A self-sustaining introgressant form with *rutilus* mitotypes and *gapperi* nuclear markers is an exclusive occupant of an 80 km wide zone between genetically pure parental species (Runck et al. 2009). For hybridisation with *glareolus,* see under that species.

Distribution (Figure 46). Boreal forest zone from north-eastern Fennoscandia to Kamchatka and Chukotka, also Alaska and northern Canada. Although largely contiguous, the range is fragmented between the Yenisey and Lena Rivers. In the Western Palaearctic, *rutilus* goes further north into the forest tundra than *glareolus*, reaching along river valleys to the shrubby tundra on the shores of the Arctic Ocean but does not

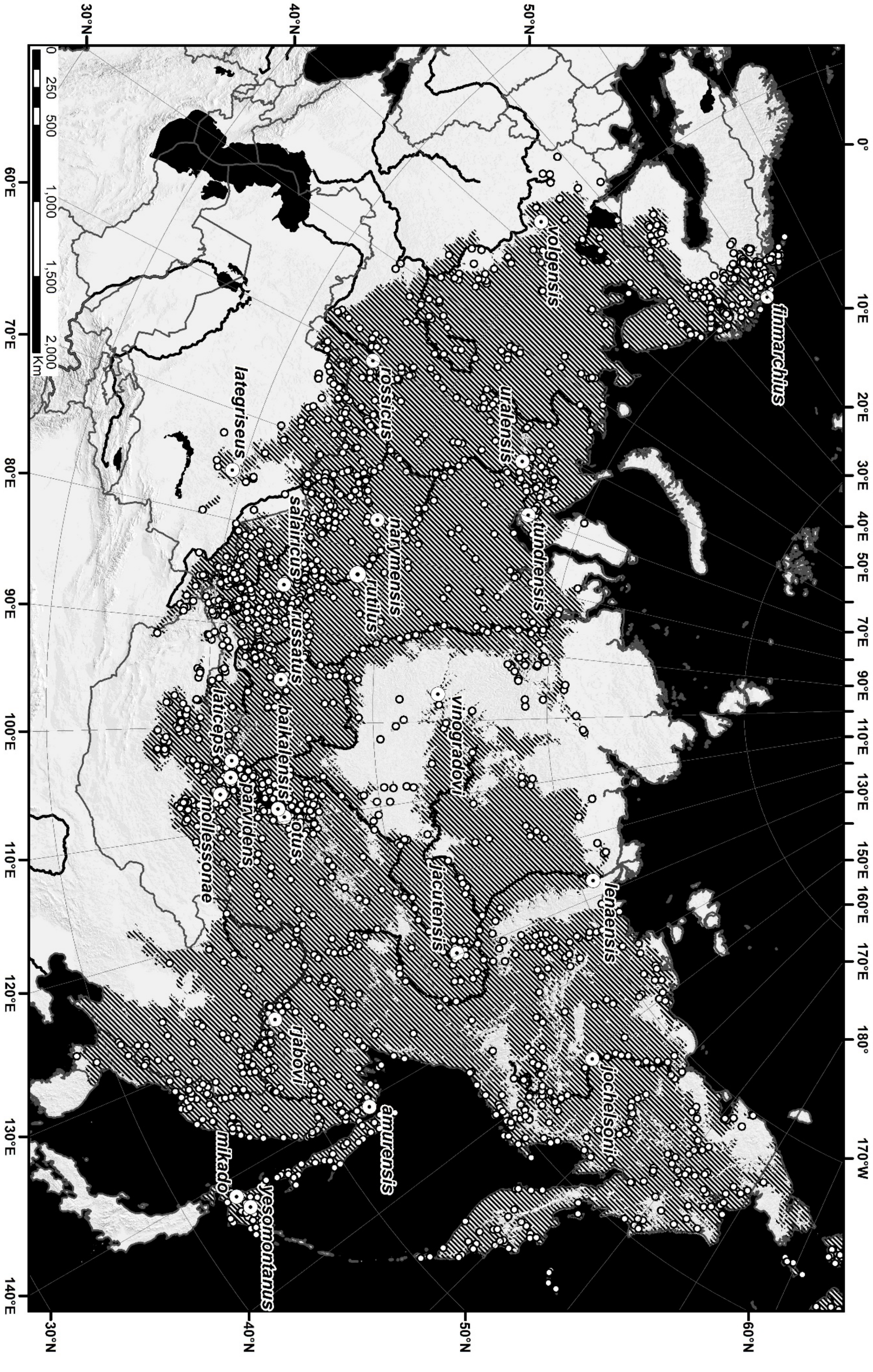


Figure 46: Distributional range of the Siberian red-backed vole *Clethrionomys rutilus* .

occupy the low arctic tundra proper. The forest-steppe zone sets the southern margin of the range. Southernmost occupancies frequently overlap with mountain habitats (forests, meadows and shrubs) in the southern Urals, central Kazakhstan, the Altai and the Sayan Mts., and with mountain chains in Mongolia, north-eastern China and North Korea. *C. rutilus* is present in several large (Sakhalin, Hokkaido) and numerous smaller islands offshore Asia (the Kuril' and the Beringia archipelagos; Kostenko 1984) and North America (MacDonald & Cook 2009). Introduced to 2 islands off Kamchatka: Bering Island (late 19th century) and Medny Island (in 1963; Bobrov et al. 2008). Elevational range is from sea level up to 1,380 m in Sakha (Russia), 1,770 m in Jilin (north-eastern China), 1,820 m in Hokkaido (Japan), 1,900 m in North Korea, 2,025 m in the Sayan Mts. (Khakasia), 2,400 m in Khangay Mts., and 2,650 m in Mongolian Altai. The entire range covers 17,572,000 km^2, 81.3% of which is in the Palaearctics.

Characteristics. *S*imilar to *glareolus* but the tail is shorter (~⅓ H&B) and more densely clothed in *rutilus* with a decidedly longer terminal pencil (Figure 41c). Dimensions: BWt = 18 – 43 H & B = 95 – 117 mm, TL=25–55 mm, HF=15–20 mm, EL=10.5–16 mm, CbL=22.0–26.7 mm, ZgW=12.6–14.5 mm, MxT=4.5–6.6 mm. Mantle is bright reddish-brown to chestnut (locally darkened by black-tipped hairs) and is frequently clearly demarcated from greyish rusty-yellow flanks; ventral side is whitish to whitish grey, often washed buff. Winter pelage is brighter. Some populations have entirely lost the rusty tint and those from the floodplains of central Yenisey and Amur are dorsally deep wood-brown to blackish-brown. The tail is sharply bi-coloured in the majority of individuals and the upper side is rufous to dusky. Baculum is long and slender; distal processes are relatively short; mean length of the proximal baculum is 2.9 mm in Alaska (Hooper & Hart 1962) and 2.5 mm in Japan (Yato & Motokawa 2021). Sperm head is longer (length=7.4–8.0 μm) than in *C. glareolus* and thinner at the base (Smirnov et al. 2021). The skull tends to retain juvenile shape and molars develop roots at the age of ~5–6 months, i.e. considerably later than in *C. glareolus*. Skull is shallower and the mandible more slender than in *glareolus* (Figure 43). Posterior edge of the hard palate is frequently interrupted (e.g. in ~60% of individuals from Siberia). M^3 is relatively longer than in *glareolus*, usually with 4 salient angles on the lingual side; other variants occur in up to 5% (3 angles) and up to 20% (5 angles) of individuals from Russia (Ognev 1950); the corresponding percentages in Hokkaido are 0.3% and 1.8% (Nakatsu 1982). The anterior loop is more compressed than in *C. glareolus* (Ognev 1950). Moreover, the M_1 is usually relatively longer and the isthmus between the anterior cap and antero-lingual triangle T5 is narrower in *rutilus* than in *glareolus* (Figure 44e'). Karyotype: 2n=56, NF=58–60, NF_a=56, X is large acrocentric, Y is small metacentric, rarely acrocentric (Orlov et al. 1978, Zima & Král 1984, Sokolov et al. 1990).

Variation and subspecies. Shenbrot & Krasnov (2005) listed 18 subspecies, 8 of which are from the Palaearctic region; Bolshakov & Shwarz (1965) recognised 4 subspecies (the nominal, *jochelsoni, lategriseus, tundrensis*) in Russia. On the other extreme, Tokuda (1941) and Rossolimo (1962) believed that high individual variation in morphological traits combined with low divergence among populations is poor grounds for recognition of categorical geographical races. Island populations do not deviate noticeably from the mainland ones (Bolshakov & Vasilyev 1976). The Y chromosome is bi-armed throughout the range except in southern Siberia where it is acrocentric (Zima & Král 1984, Sokolov et al. 1990).

Molecular evidence retrieved 3 parapatric lineages with secondary contact zones between them. These lineages split <100 kya. The majority of the Palaearctics is occupied by 2 lineages (West and Central), roughly delimited by the Yenisei River. Another lineage, the Beringian, occupies both sides of the Bering Strait and is further structured into 3 sublineages: trans-Beringian (Kamchatka and the Nearctic range) and two insular sublineages, occurring in Sakhalin and Hokkaido, respectively (Kohli et al. 2014).

Clethrionomys centralis (Miller, 1906) – Tien Shan Red-backed Vole

Evotomys centralis Miller, 1906: 373. Type locality: "Koksu Valley, altitude 9000 feet [2,743 m]", eastern Kazakhstan.

Synonyms. *Evotomys frater* Thomas, 1908.

Taxonomy. Kirikoff (1935) synonymised *centralis* (*frater*) with *glareolus* (accepted in Corbet 1978) and Gromov & Baranova (1981) synonymised it with *rutilus* (followed by Zhang et al. 1997). Rossolimo (1963) argued that *centralis* is a species in its own right. Genetic analyses placed *centralis* closer to *glareolus* (Tang et al. 2018) than to *rutilus*. Differences between *centralis* and *glareolus* are also obvious in acoustics (Rutovskaya 2019a).

In the past, *centralis* and *frater* were occasionally held as 2 distinct species (Hinton 1926a, Vinogradov & Argyropulo 1941) and Chinese authors continued this practice until recently (Ma et al. 1987, Hou et al. 2000, Luo et al. 2000, Wang 2003). Vinogradov & Argyropulo (1941) distinguished between the two taxa using the hairiness of their tails: *centralis* resembles *glareolus* while *frater* is closer to *rutilus*. In the past, Russian authors frequently reported this species as *frater* (e.g. Ognev 1950, Gromov & Polyakov 1977, Sludskiy et al. 1978).

Distribution (Figure 47). Tien Shan and Dzungarian Alatau in south-eastern Kazakhstan, Kyrgyzstan and north-western Xinjiang (China). Range area is ~84,755 km^2. Species is tied to the forest zone at 1,110–2,890 m a.s.l. (exceptionally down to 600–800 m; Sludskiy et al. 1978).

Characteristics. Similar to *glareolus* in size and proportions but differs in colour. Back is ochraceous-buff to rich brown, darkened by blackish hair tips, "with only enough rufous suffusion to indicate that it is an *Evotomys* [=*Clethrionomys*]" (Thomas 1908a:448); underparts are light smoke grey, frequently washed buff. Tail is moderately long (TL/H&B=0.40–0.53),

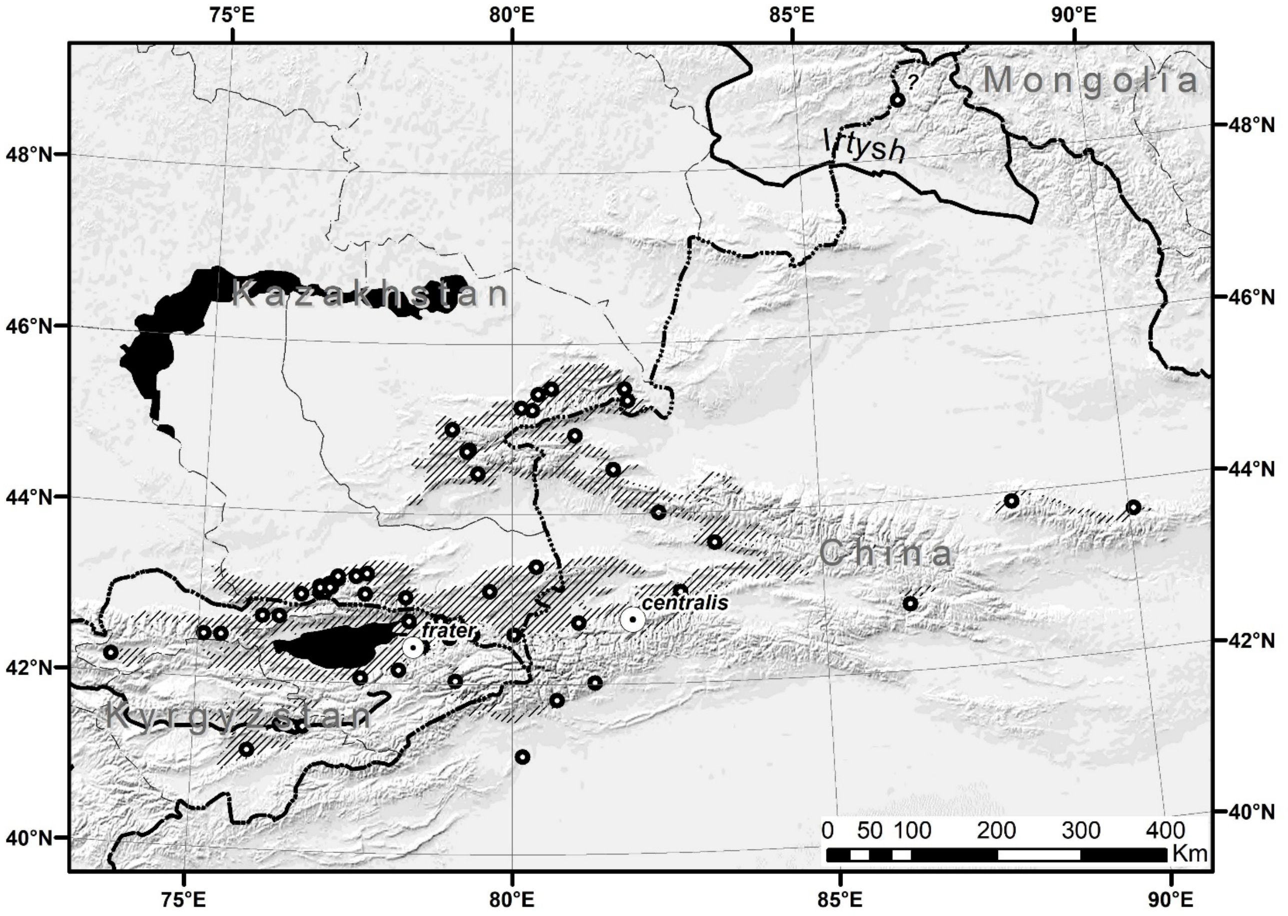


Figure 47: Distributional range of the Tian Shan red-backed vole *Clethrionomys centralis*. The outlying record in northern Xinjiang (from Tang et al. 2018) is most likely incorrect (indicated by the question mark).

moderately hairy (Figure 41b) and sharply bi-coloured; dorsal side is darker than in *glareolus*, frequently black-brown; terminal pencil is longer (usually > 6 mm) than in *glareolus* (usually <5 mm). The baculum is robust with a relatively short and heavy stalk and massive distal processes (Ognev 1950). Skull and dentition as in *glareolus* (Figure 44) except for a less curved and longer alveolar sheath of the upper incisor. M^3 usually with 3 (rarely 4) inner salient angles (Sludskiy et al. 1978). Karyotype: 2n=56, NF=60, NF_a=56, the X is large acrocentric, the Y is small metacentric or acrocentric (Dimitriev 1990, Sokolov et al. 1990).

Variation and subspecies. Gromov & Erbajeva (1995) considered *frater* subspecifically distinct from *centralis* but Sludskiy et al. (1978) did not recognise subspecies in Kazakhstan.

GENUS: *Alticola* Blanford, 1881 – Mountain Voles

Taxonomy. Blanford (1881b) established *Alticola* as a "section" (rank comparable to a subgenus) of *Arvicola* that during his time encompassed all arvicolines except lemmings. Sclater (1891) still followed Blandford's arrangement but Thomas (1912b) and Miller (1912b) simultaneously endorsed *Alticola* as a genus in its own right. A generic rank was soon uniformly adopted (e.g. Hinton 1926a, Vinogradov 1933, and subsequent authors); the inclusion of *Alticola* in *Microtus* by Allen (1924) was a short-lived and futile attempt. The taxonomic scope of the genus remained relatively stable ever since Vinogradov's (1933) incorporation of *Aschizomys* in *Alticola.*

In the past, *Aschizomys* was frequently associated with *Clethrionomys, Craseomys* or *Eothenomys.* In Miller's view (1899b:368), *Aschizomys* "combines the peculiarities of these two genera [*Microtus* and *Clethrionomys*] so perfectly that it is necessary either to recognise the new form as an annectant genus, or to reduce *Evotomys* [=*Clethrionomys*] to the rank of a subgenus of *Microtus*, and treat the Plover Bay animal [= the type of *Aschizomys lemminus*] as still another genus." Miller opted for the latter but subsequently changed his view (Miller 1940) and allocated *Aschizomys* to *Clethrionomys,* a step followed in Ellerman & Morrison-Scott (1951). In the opinion of Hinton (1926a:43), *Aschizomys,* which was still known to him only from the type, was "not of generic value" being rather "a more or less aberrant member of the *E.* [=*Craseomys*] *rufocanus* group". With new material at hand, Vinogradov (1927) categorically rebuffed this suggestion and subsequently (Vinogradov 1933) downgraded *Aschizomys* to a subgenus of *Alticola.* The vast majority of authors accepted Vinogradov's view; Corbet (1978:100), however, disagreed and included *Aschizomys* to *Eothenomys* "because the molar pattern is much closer to *Eothenomys* than to *Alticola*" (followed in Aimi 1980, and Honacki et al. 1982). Phylogenetic reconstruction based on *Cytb* excluded *Aschizomys* from the scope of *Alticola* and aligned it with *Clethrionomys* (Cook et al. 2004, Lebedev et al. 2007). Of the 2 species of *Aschizomys, lemminus* was retained under that generic name while *macrotis* was included in *Clethrionomys* (Pardiñas et al. 2017). Mitochondrial branching typologies, however, did not reflect the true phylogeny due to ancient introgression of the *Mt*-genome from *Clethrionomys; macrotis* possibly captured *Mt*-DNA from *C. centralis* as did *lemminus* from *C. rutilus* (Kohli et al. 2014). Nuclear genes confirmed the sister position of *Alticola* and *Ascizomys* (Kohli et al. 2014, Bodrov et al. 2016) which are ranked here as a subgenera of *Alticola.*

Distribution. *Alticola* is endemic to Central and north-eastern Asia where it is usually found in mountain ranges and plateaus between the Hindu Kush, western Tien Shan and Pamiro-Alai, and central Kazakhstan in the west, the Himalayas in the south, the shores of the Sea of Okhotsk and the Chukotka Peninsula in the east, and the shores of eastern Siberia in the north. All species depend on rocky situations, specifically screes, accumulations of rocks and boulders, cracks in cliffs, escarpments, shafts and crevices in rocky substrate. The altitudinal range is from sea level up to 6,140 m a.s.l. (see under *A. stoliczkanus*); mountain voles are found at higher altitudes than any other arvicolines.

Closely related rock-dwelling (petrophilous) small mammals coexist with difficulty and species tandems of mountain voles are only rarely found in sympatry.

Characteristics. Small to medium large voles with comparatively large ears, long whiskers (Figures 67, 76), and soft, greyish pelage. The individual hairs are slaty for the greater portion of their length with a subterminal band of buff or brown and a minute blackish tip. Ventral hairs are deep slaty at the base with white tips; the dark bases appear irregularly at the surface. Tail is highly variable (Figure 48), from very short to long. In many species the tail is densely clad with stiff hair that conceal the scales; pencil is usually prominent (>10 mm). Palms and soles have 5 and 6 pads, respectively; the latter are hairy from the heel to the posterior pad. Medial metatarsal pad is of approximately the same size as the interdigital pads (Figure 49). Length of the toes vary from short (*stoliczkanus*; Figure 49b) to relatively long (*argentatus*; Figure 49c). Females have 8 nipples.

The skull is of typical Clethrionomyini proportions (ZgW/CbL=0.52–0.60). It is excessively flat in some representatives of the subgenus *Alticola*, most extremely in *strelzovi* where the height behind M^3 is <25% CbL (Figure 68). A shallow skull is combined with a low

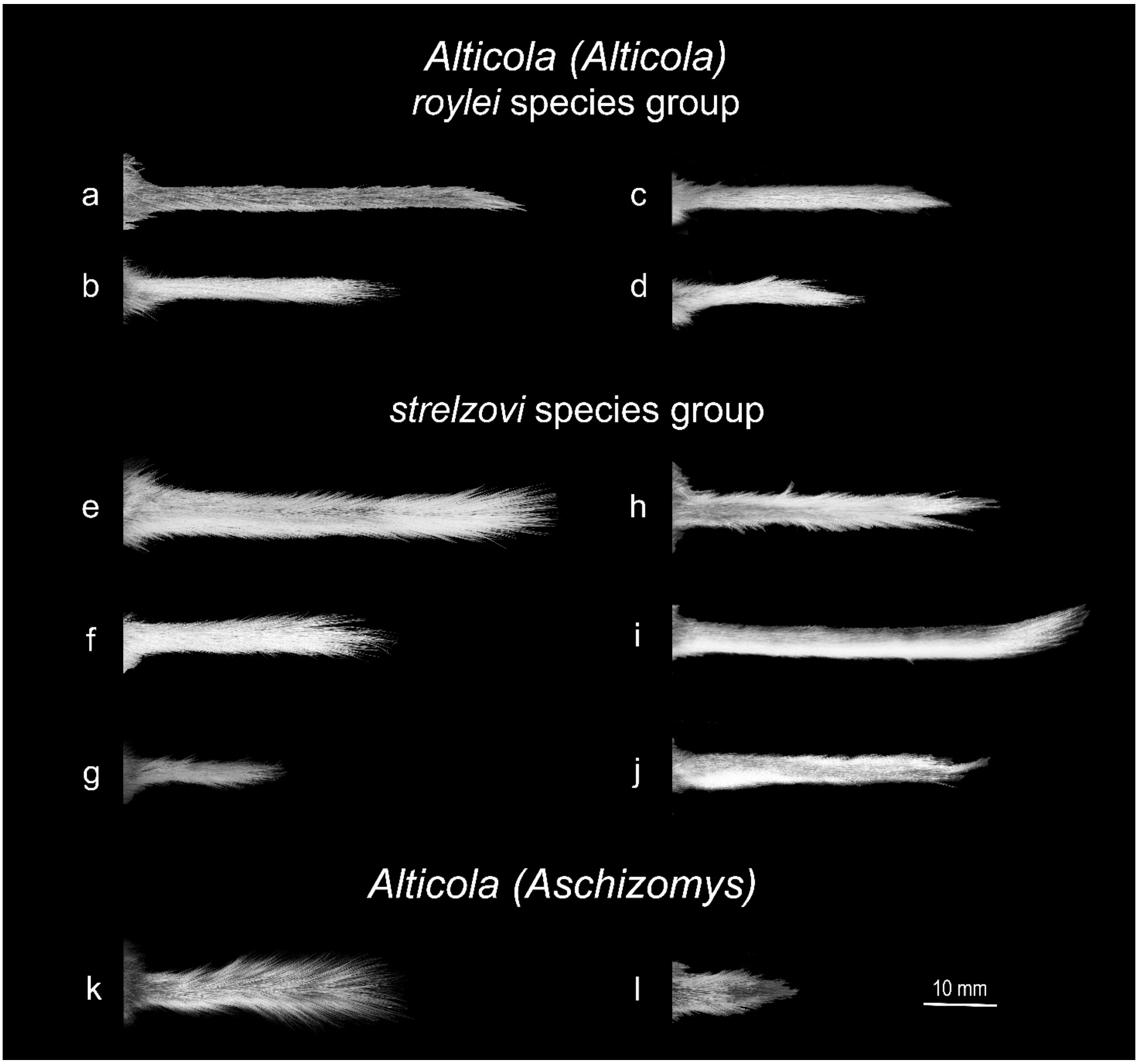


Figure 48: Tail in mountain voles *Alticola* (dorsal view): a–*A. roylei* (from Pisang, Mt. Anapurna, Nepal); b–*A. albicauda* (Phyang Nullah, Ladakh, India); c–*A. argentatus tarasovi* (Sary, E Kyrgyzstan); d–*A. stoliczkanus* (Kashmir, India); e–*A. strelzovi* (Tashanta, Kosh-Agach, Altai Republic, Russian Federation); f–*A. semicanus* (Chousgol-Aimak, Darkhat Basin, Mongolia); g–*A. barakshin* (Gobi-Altayskiy aymak, Tayshiryn-Nuru, Mongolia); h–*A. tuvinicus tuvinicus* (nr. Uyuk, Tuva, Russian Federation); i– *A. tuvinicus khubsugulensis* (Lake Khubsugol, Mongolia); j–*A. olchonensis* (Olkhon Is. on Lake Baikal, Russian Federation); k–A. *macrotis* (Ivanovskie Belki, Ridder, Kazakhstan); l–*A. lemminus* (Koryak Territory, Russian Federation). Photo B. Kryštufek.

mandibular corpus and ramus. Posterior palate is like in *Clethrionomys* and palatal foramina are long (Figure 9a). Temporal ridges remain widely separated in adults; the squamosal crest is usually poorly developed and bullae are large, inflated, and lack spongy tissue. Molars are rootless; enamel pattern differs markedly between the subgenera (see descriptions hereinafter).

Karyotype is conservative and all silver voles studied karyologically thus far have displayed an identical conventionally stained set of predominantly acrocentric chromosomes (2n=56).

Key to species

1a) Salient angles rounded, re-entrant angles abundantly filled with cement; T2 on M^3 is normally developed and isolated from AL. Incisive foramina short, terminating well before the level of M^1 anterior edge ………………………………… 2 (subgenus *Aschizomys*)
1b) Salient angles pointed, re-entrant angles with little or no cement; T2 on M^3 is usually rudimentary and integrated in AL. Incisive foramina longer, terminating approximately at the level of M^1 anterior edge ………………………………… 3 (subgenus *Alticola*)
2a) Winter pelage always grey-brown (like the summer pelage); tail longer (TL/H&B usually >0.2); M^3 usually with 3 lingual salient angles and confluent dental fields ……………………………………………….. *macrotis*
2b) Winter pelage either grey-brown or white; tail shorter (TL/H&B usually <0.2); M^3 usually with 4 lingual salient angles and with at least some of the dental fields isolated ……………………………….. *lemminus*
3a) Triangle T2 on M^3 normally developed and isolated from AL; M^3 usually with 3 deep re-entrant angles on each side; on M^2, labial re-entrant angles visibly deeper than the lingual ones; pelage deep wood-brown ………………………………………………. *montosus*
3b) Triangle T2 on M^3 is rudimentary and confluent with AL; M^3 normally with lingual re-entrant angles as deep as the lingual ones; pelage variable but usually with plain grey tints ……………………………………… 4
4a) Tail short (TL≈HF); M^3 with 1 deep re-entrant angle on the lingual side, T5 absent or rudimentary ……… 5

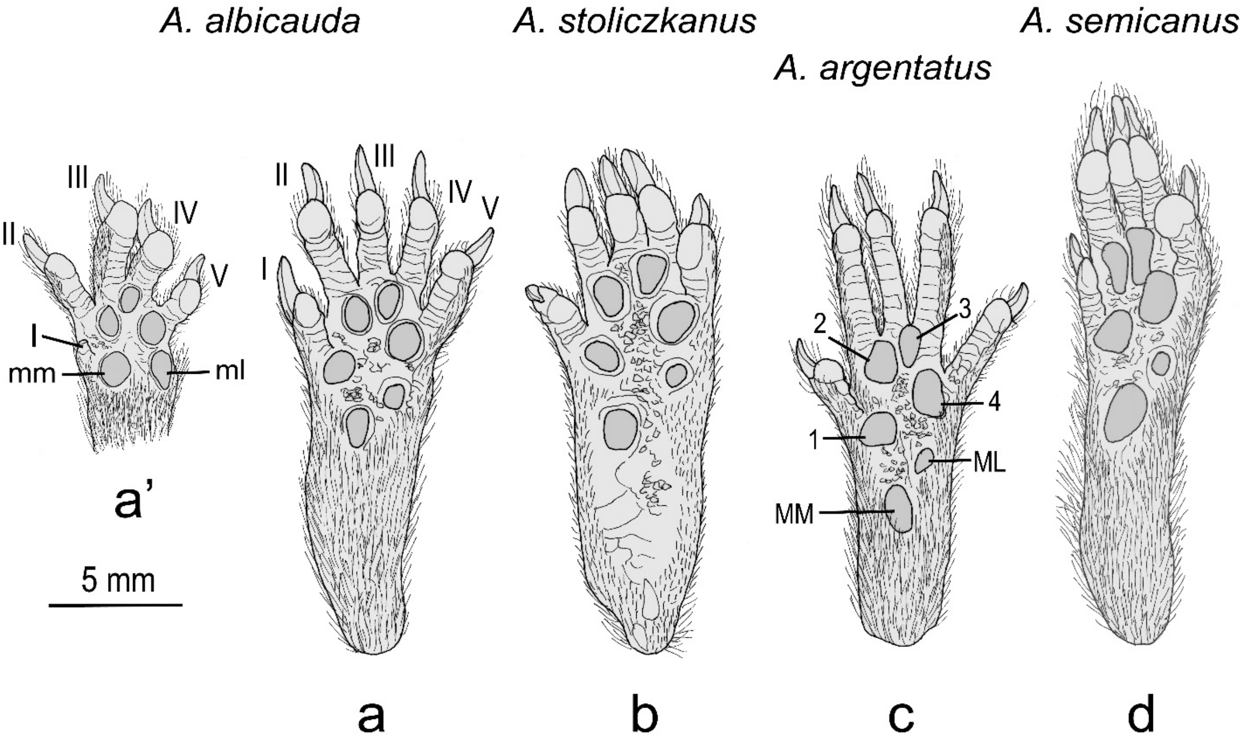


Figure 49: Left palm (a') and sole (b–e) in mountain voles: a–*Alticola albicauda* (Liligo, Paju, Broad Peak, Pakistan); b–*A. stoliczkanus* (Nashingala, Kashmir, India); c–*A. argentatus* (northern Pakistan); d–*A. semicanus* (Barun-Urt env, Mongolia). Digits are indicated using Roman numbers (thumb=I) and interdigital pads are represented by Arabic numbers. Metacarpal and metatarsal pads are specified by lower (m) and upper case letters (M), respectively: mm/MM—medial pad, ml/ML—lateral pad.

4b) Tail longer (TL>HF); M^3 with at least 2 deep re-entrant angles on the lingual side. T5 prominent …… 6

5a) Braincase relatively short; M^3 not laterally compressed, length of PC>56% M^3 length; present in the Tibetan Plateau and the Himalayas ….... *stoliczkanus*

5b) Braincase relatively long; M^3 laterally compressed, length of PC<57% M^3 length; present north of the Tibetan Plateau …………………………….. *barakshin*

6a) Skull shallow, height behind M^3 <31% CbL; present mainly north of 44^0N latitude ………………………. 7

6b) Skull deep, height behind M^3 >29% CbL; present mainly south of 44^0N latitude …………………….. 10

7a) Height of skull behind M^3<26 CbL; dorsal profile concave; middle lacerate fossa enlarged; M^3 laterally compressed ………………………………….. *strelzovi*

7b) Height of skull behind M^3>26% CbL; dorsal profile straight (in some individuals slightly concave); middle lacerate fossa not enlarged; M^3 not laterally compressed …………………………………………………... 8

8a) M^3 with very short posterior cap (length of PC<width of AL) ………………………………….. 9

8b) M^3 with longer posterior cap (length of PC≈width of AL) ……………………………………….. *tuvinicus*

9a) Tail white throughout; BR2 of M^3 is shallow ……………………………………………… *semicanus*

9b) Tail bi-coloured, dark above, light below; BR2 of M^3 is deep and square-like ……………………... *olchonensis*

10a) MxT/CbL>0.24; upper incisors slightly proodont; pelage usually dark (wood brown) ………………. *roylei*

10b) MxT/CbL<0.26; upper incisors orthodont; pelage lighter ……………………………………………... 11

11a) TL/H&B<0.34; tail densely haired with long (> 10 mm) pencil; demarcation on the flanks is sharp ……………………………………………… *albicauda*

11b) TL/H&B>0.33; tail usually lightly haired with feeble pencil; demarcation on the flanks not sharp … 12

12a) Endemic to the Hindu Kush Mts. ……….*parvidens*

12b) Occurs elsewhere …………………………….. 13

13a) Tail is lightly coloured; present north of the Gilgit River; some individuals have inner cheek pouches …………………………………………... *argentatus*

13b) Tail is sharply bi-coloured (blackish-brown above); present south of the Gilgit River ……. *kohistanicus* n. sp.

SUBGENUS: *Alticola* Blanford, 1881

Alticola Blanford, 1881b:96. Proposed as a section of *Arvicola*. Type species by subsequent designation (Miller 1896:52) is *Arvicola stoliczkanus* Blanford.

Synonyms. *Platycranius* Kastschenko, 1901.

Taxonomy. Hinton (1926a) proposed an excessive split of *Alticola* into 14 species; 4 of his names are synonyms of *stoliczkanus* and *argentatus*, respectively, and a further 2 names are in *montosus*. Ellerman & Morrison-Scott (1951), on the other hand, recognised merely 3 species: *strelzovi* (with a flat skull), *stoliczkanus* (M^3 simple) and *roylei* (M^3 complex). Rossolimo & Pavlinov (1992) distinguished 8 species (in addition to *strelzovi*) in a meticulous revision of the subgenus. We recognise 12 species based on their revision and subsequent molecular phylogenetic trees (Lebedev et al. 2007, Bodrov et al. 2016, Tang et al. 2018, Bhatt 2020).

Molecular trees retrieved 2 supported lineages with strong geographic associations hereafter ranked as species groups. The *roylei* species group (*albicauda, argentatus, montosus, parvidens, roylei, kohistanicus* sp. n.) is characterised by a deeper skull and occupies the south-western part of the range. The *stoliczkanus* species group (*barakshin, olchonensis, semicanus, strelzovi, tuvinicus, stoliczkanus*) has a shallower skull and occupies the northern and south-eastern part of the range. Traditionally, *Alticola* s. str. was split into 2 subgenera: *Platycranius* (with *strelzovi*) and the nominal subgenus with the remaining species. Although *strelzovi* has a strikingly different cranium, it is nested inside the *stoliczkanus* species group as a sister species to *semicanus* (Bodrov et al. 2016).

Distribution. The southern part of the range of the genus. Ranges of *Alticola* s.str. and *Aschizomys* overlap in the Altai, the wider area of Lake Baikal, and northern Mongolia.

Characteristics. Medium-sized to moderately large voles with dense, soft and usually long fur. Eyes are moderately large and simple, rounded ears usually overtop the pelage. There are 5 palmar and 6 plantar pads; females have 8 nipples. Molars tend to be compressed laterally with little or no cement in the re-entrant angles; dental fields are symmetrical and alternate. The M^3 has 1–3 re-entrant angles on the lingual side and 2–3 on the labial side; the antero-labial triangle T2 is reduced and widely confluent with the anterior lobe (except in *montosus*). The subgenus is unique among Clethrionomyina in having a positive enamel differentiation; in *argentatus,* the thickness of the anterior band on M_1 is 0.06 mm, and the posterior band is 0.02 mm thick. The schmelzmuster always contains at least some lamellar enamel, mainly in the concave (luff) edges of triangles (Koenigswald 1980, Robovský et al. 2008).

The karyotype (2n=56) is uniform (known in *argentatus, barakshin, semicanus,* and *strelzovi*), This uniformity, along with the rarity of interspecific rearrangements, suggests a conservatively fixed karyotype (Hielscher et al. 1992).

Species group *roylei*

Alticola roylei (Gray, 1842) – Royle's Mountain Vole

Arvicola roylei Gray, 1842:265. Type locality ("India (Chasmere) [Kashmir]") is erroneous since *roylei* does not occupy Kashmir. Wroughton (1914:299) argued that the type originates from "the higher Ranges of Kumaon" Uttarakhand, India (see also Wroughton 1920:59). Hinton (1926a:313) accepted Wroughton's fixation.

Synonyms. *Alticola blanfordi lahulius* Hinton, 1926; *Alticola roylei cautus* Hinton, 1926.

Taxonomy. Ellerman & Morrison-Scott (1951) defined *A. roylei* to encompass long-tailed mountain voles with a complex M^3 pattern and deep skull. Many of these voles are now classified as species in their own right. The current scope follows Rossolimo & Pavlinov (1992)

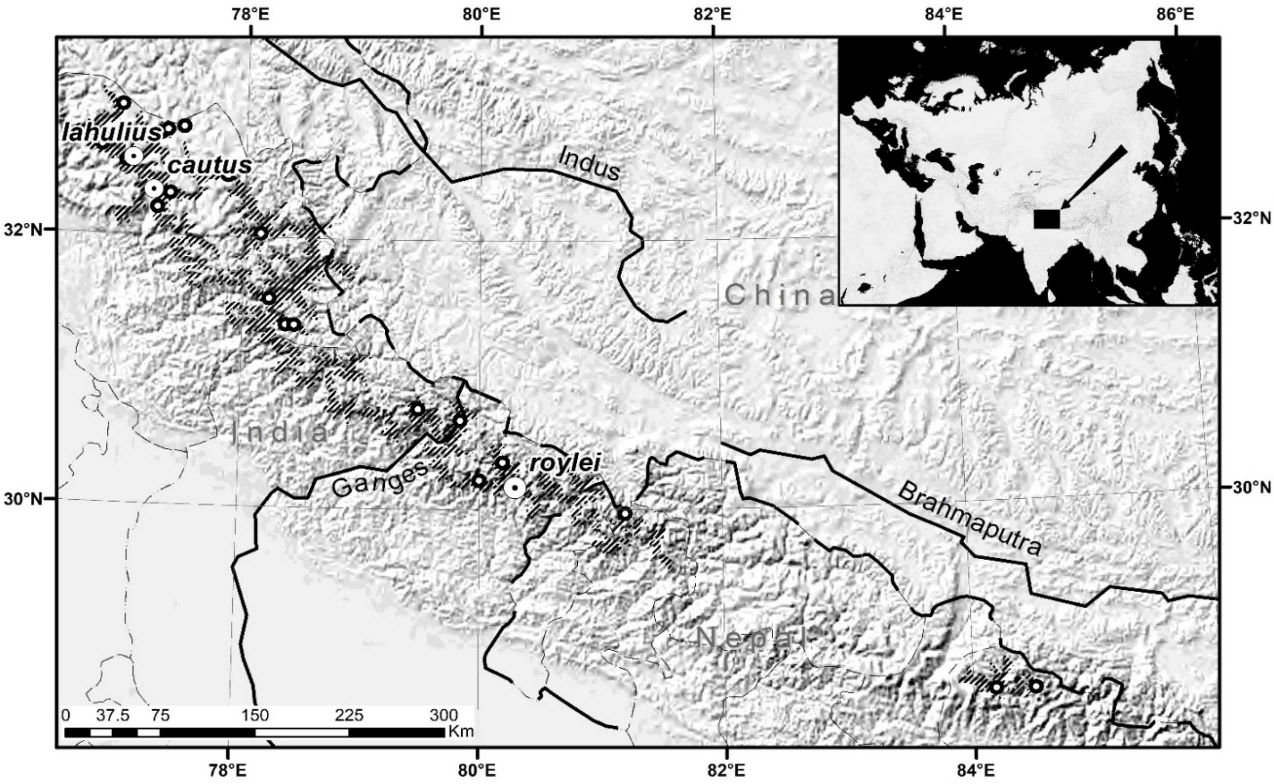
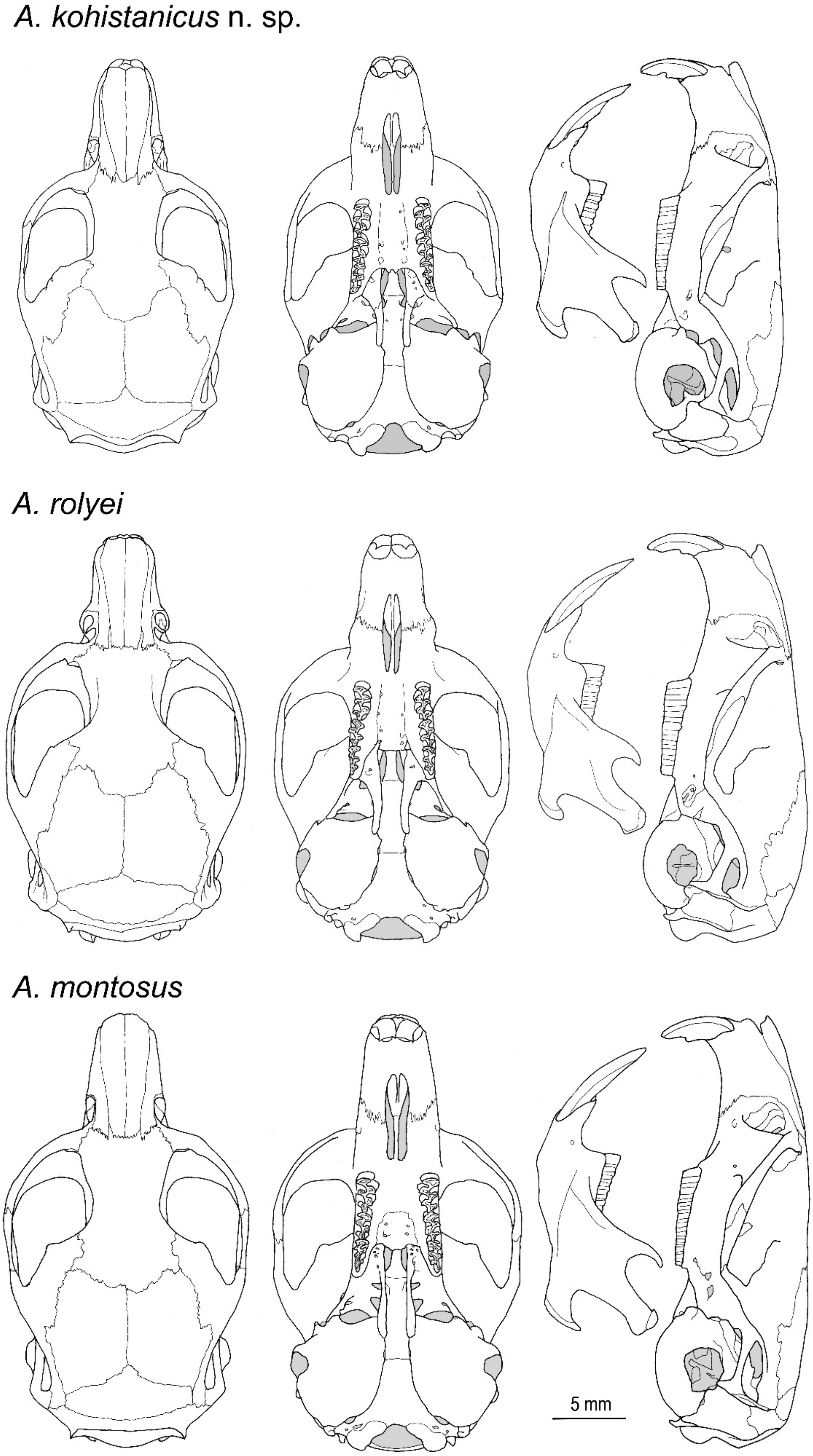


Figure 50: Distributional range of Royle's mountain vole *Alticola roylei*.


A. kohistanicus n. sp.

A. rolyei

A. montosus

Figure 51: Skull in mountain voles: top–*A. kohistanicus* n. sp. (Tangir Valley, Diamir, Gilgit-Baltistan, Pakistan); middle–*Alticola roylei* (Pisang, Dhukure Pokhari, Mt. Anapurna, Nepal); bottom–*A. montosus* (Mai Dun, Kashmir, India).

who restricted *roylei* to "Kashmir". Musser & Carleton (2005) synonymised *lahulius* with *argentatus*; because the type of *lahulius* displays relatively small bullae and a long maxillary tooth-row, we treat it as part of *roylei* (see also Kryštufek et al. 2017).

Distribution (Figure 50). Records that can be safely linked with the species come from the south-western slopes of the Himalayas between Himac Chumba and Dhar Than Pattan in Himachal Pradesh (northern India) and Pashchimanchal in central Nepal (Kryštufek et al. 2017), and spread across an area of approximately 15,290 km^2. Further Indian and Pakistani records of *roylei* are of dubious taxonomic reliability and may refer to *montosus* (e.g. Sahi 1988) or *argentatus* (Awan et al. 2004). The geographic range of *A. roylei* is therefore poorly documented and its borders are uncertain. The species is likely also present in south-western Xizang (Zhada Xian, China). Specimens were recorded from rocky habitats above the timberline at 2,800–4,715 m a.s.l.

Characteristics. Dimensions: BWt=24–30 g, H&B=91–117 mm, TL=29–48 mm, HF=17–21 mm, EL=12.5–15 mm, CbL=24.5–27.1 mm, ZgW=15.1–15.9 mm, MxT=5.8–7.2 mm. *A. roylei* is characterised by a combination of dark brown dorsal fur and a moderately long tail (TL/H&B=0.30–47), bowed zygomatic arches, small bullae, and moderately complex M^3 with three lingual salient angles. The pelage is moderately long (~13 mm), yellowish-brown, light greyish-brown or dark brown above, whitish to silvery grey (occasionally washed buff) below. The tail is distinctly bi-coloured and moderately hairy with only partly concealed underlying annulations (Figure 48a).

Skull is weakly ridged with feeble squamosal processes and a slight depression in the inter-orbital region (Figure 51); zygomatic arches are moderately expanded (ZgW/CbL=0.57–0.60). Incisive foramina reach behind the level of the anterior margin of M^1 alveoli; auditory bullae are small. Skull is deep (height behind M^3/CbL=0.30–0.34) with a bent dorsal profile. Maxillary tooth-row is relatively long (MxT/CbL=0.25–0.27); it is relatively shorter in various subspecies of *A. argentatus* (0.22–0.25) and in all mountain voles, synonymised with *roylei* at one time or another and residing north of the Takla Makan and Gobi Deserts: 0.20–0.25 in *semicanus*, 0.22–25 in *tuvinicus*, and 0.23–0.25 in *olchonensis*. Incisors are more proodont in *A. roylei* than in other mountain voles. M^3 has 3 inner and outer salient angles, respectively; a shallow 4th labial salient angle is rarely present. The antero-lingual triangle (T3) is normally isolated and PC is short, rarely of moderate length (Figure 52).

Variation and subspecies. Monotypic species (Rossolimo & Pavlinov 1992).

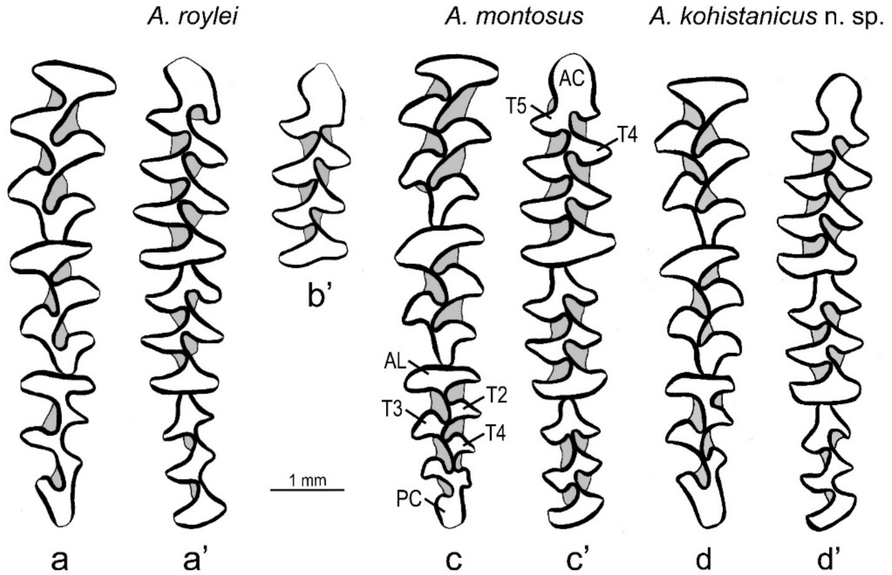


Figure 52: Molar pattern in mountain voles. *Alticola roylei*: upper (a) and lower row (a'–Manaslu, Nepal); isolated M$_1$ (b'–Kulu Valley, Lahul, India). *A. montosus*: upper (c) and lower row (c'–Liddar Valley, Pahalgam, Kashmir, India). *A. kohistanicus* n. sp.: upper (d) and lower row (d'–Khanbari Valley, Diamir, Gilgit-Baltistan, Pakistan).

Alticola montosus (True, 1894) – Kashmir Mountain Vole

Arvicola montosa True, 1894:11. Type locality: "Central Kashmir, 11,000 feet [3,350m]", northern India.

Synonyms. *Microtus imitator* Bonhote, 1905.

Taxonomy. Regarded in the past as a subspecies of *roylei* (Ellerman 1941, 1961, Ellerman & Morrison-Scott 1951, Heptner & Rossolimo 1968); restored as a species in its own right in Rossolimo & Pavlinov (1992). In phylogenetic trees, *montosus* holds a sister position against *argentatus*+*albicauda* (Tang et al. 2018).

Distribution (Figure 53). North-eastern Pakistan to the south of the Indus River (Azad Kashmir, easternmost North-West Frontier Province and south-eastern part of the Northern Area) and northern India (western Jammu and Kashmir). The record for Afghanistan (Zimmermann 1955, Chakraborty 1983, Agrawal 2000) is erroneous. The Kashmir mountain vole occupies rocky habitats on slopes and in river valleys; specimens were also trapped in the forest, jungle and inside houses (Ellerman 1961). Altitudinal range is from 1,965 m (Mai Dunn) to 4,350 m a.s.l. (Dachin, Khistwar), and the distributional range is estimated at 26,750 km2.

Characteristics. A large mountain vole: BWt=37–49 g, H&B=102–126 mm, TL=41–65 mm, HF=17.5–22.9 mm, EL=13–17 mm, CbL=25–27.9 mm, ZgW=14–15.9 mm, MxT=6–7.1 mm; tail is moderately long (TL/H&B=38–39). Fur is long (up to 12 mm on midback) and soft. Back is dull greyish-brown; underparts are silvery grey, darkened by slate basal portion of the fur and without any marked buffy suffusion. Grey flanks contrast the brown back although there is no sharp delimitation. Ears are blackish-grey; tail is faintly bi-coloured, dusky above, whitish below with hairs which are too few and too short to conceal the annulations; terminal pencil is very short. Feet are greyish. Skull is weakly crested with prominent squamosal processes (Figure 51), expanded zygomatic arches (ZgW/CbL=0.52–0.59), short braincase (width≈length), wide interorbital region and short incisive foramina (not reaching the level of M^1 alveoli). Maxillary tooth-row is moderately long (MxT/CbL=0.23–0.26). Braincase is as deep as in *roylei*; bullae are moderately large (Figure 51). M^3 is longer than M^2 with 4 salient angles on each side (Figure 52c); triangle T2 is large and usually isolated from the anterior loop; dental fields T3–4 are well-developed and isolated; posterior lobe (heel) is short. M_1 is simple, T5–6 are confluent with anterior loop. M^1–M^2 have buccal re-entrant angles deeper than the lingual loops.

Variation and subspecies. Monotypic species (Rossolimo & Pavlinov 1992).

Alticola kohistanicus new species – Kohistan Mountain Vole

Taxonomy. Mountain voles from Diamir and Swat Districts of Gilgit-Baltistan, northern Pakistan, constitute a unique *Mt*-clade (the Eastern Kohistan Clade sensu Bhatt 2020) which is in a sister position with respect to the Great Himalayan Clade (=*montosus*). These clades share TMRCA at 0.97 Mya (CI=0.53–1.84 Mya) which is within the range for species divergences in mountain voles. No name is available for mountain voles sandwiched between the Gilgit and Indus Rivers, hence we designate the Kohistan clade of mountain voles as a new species.

Holotype. Adult female (Florida Museum of Natural History, University of Florida, FU 22759), flat skin and skull, Collected by M. Rafique on October 12, 1995. Tissue sample is deposited at the University of Vermont (UVM 876; Bhatt 2020).

Type locality. Pakistan, Gilgit-Baltistan (formerly Northern Areas), Diamir District, Tangir Valley, 35.8539N, 73.3664E, 2,900 m above sea level.

Etymology. Named after the Kohistan Range where the type comes from.

Description. Size is small; tail is short (TL/H&B=0.35–0.36). Fur is 9–10.5 mm long and the scant protruding hairs are only slightly longer. Dense hair on the tail conceals the annulation and terminates in a 6–6.5 mm long apical pencil. Dorsal fur is brown with no greyish hue; flanks are lighter. The belly is

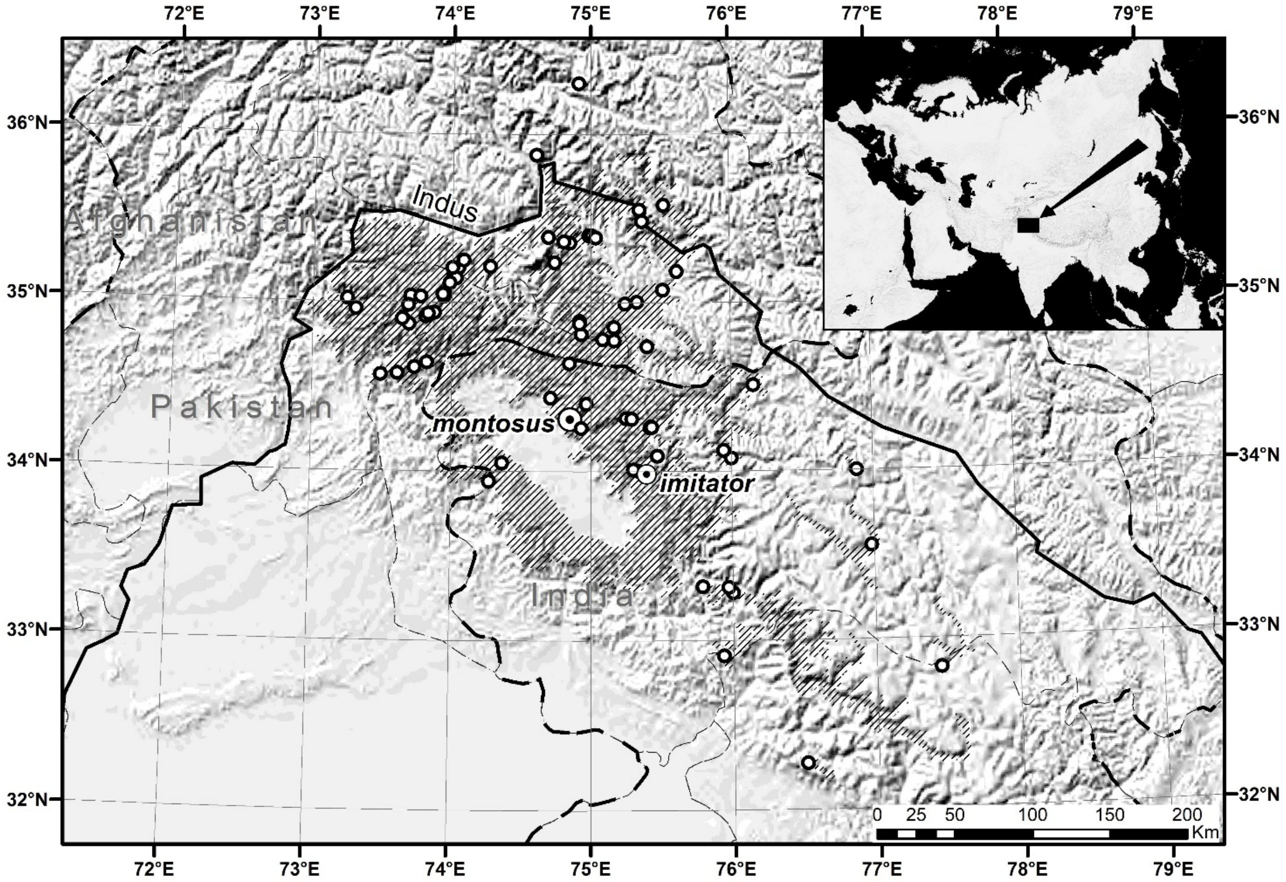


Figure 53: Distributional range of the Kashmir mountain vole *Alticola montosus*.

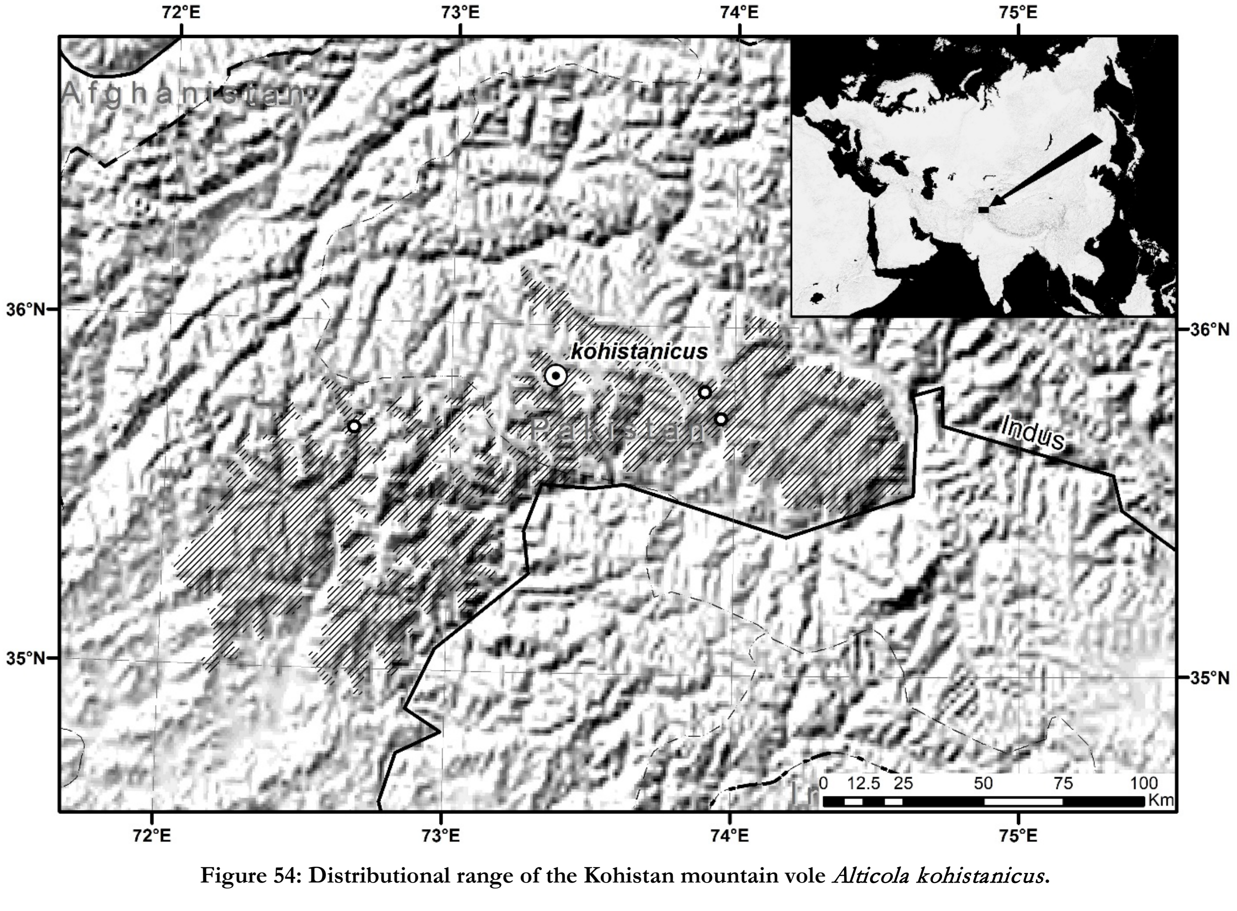


Figure 54: Distributional range of the Kohistan mountain vole *Alticola kohistanicus*.

greyish white or grey, heavily clouded by slaty hair bases; demarcation is fairly distinct. Feet are whitish or light grey, ears are grey; the tail is sharply bi-coloured, blackish-brown above, whitish or light-grey below. Skull is lightly ridged with feeble squamosal processes, zygomatic arches are rather narrow (ZgW/CbL=0.53–0.55), braincase is shallow and interorbital region is narrow (≈14–17% CbL). Bullae are of moderate size, incisive foramina are short and do not reach the level of M^1 alveoli (Figure 51), and the molar row is also short (MxT=20.7–24.8% CbL). M^3 with 2 inner re-entrant angles; dental field of T2 opens into the anterior loop; T4 occasionally confluent with the posterior loop; heel is short (Figure 53d). Dimensions of the type: BWt–24 g, H&B–111 mm, TL–39 mm, HF–20 mm, EL–14 mm, CbL–25.8 mm, ZgW–14.1 mm, MxT–6.7 mm.

Diagnosis and Comparisons. Phylogenetic analysis of *Mt*-DNA haplotypes (Bhatt 2020) retrieved *kohistanicus* sp. n. as a close relative to *montosus*. The new subspecies differs from *montosus* in greyish fur, comparatively narrower zygomatic arches, longer braincase and a slightly shorter upper row of molars. M^3 has 2 inner re-entrant angles (3 angles in *montosus*) and T2 is confluent with anterior loop; T4 is occasionally confluent with posterior loop (T2 and T4 are closed in *montosus*). Anterior margin of nasals is straight (rounded in *montosus*). Of the species present in the region, *argentatus* is externally and cranio-dentally the most similar to the new species and differs chiefly in whitish dorsal side of the tail; moreover, the pelage is usually lighter. *Alticola roylei* has more expanded zygomatic arches (ZgW/CbL>0.56% vs <0.56 in the new species), longer incisive foramens (reaching posteriorly the level of M^1), smaller bullae, and proportionally longer upper molar-row (MxT/CbL>0.24 vs <0.25 in the new species). *Alticola albicauda* has a shorter tail (TL/H&B<0.35 vs >0.35 in the new species) which is densely clad with white hairs. *Alticola parvidens* lacks deep brown tints but is otherwise of similar size and proportions.

Distribution (Figure 54). Mountains between the Gilgit and Indus Rivers in Districts of Diamir and Swat (Gilgit-Baltistan, northern Pakistan). Museum vouchers were collected from rock crevices, stone walls, and inside a pine forest.

Alticola argentatus (Severtzov, 1879) – Silver Mountain Vole

Taxonomy. In the past, the silver mountain vole was frequently treated as a conspecific of *roylei* (e.g. Ellerman & Morrison-Scott 1951, Wang 2003), or was split in 4 (Vinogradov 1933, Ellerman 1941) or 5 species (*argurus, blanfordi, glacialis, phasma,* and *worthingtoni*; Hinton 1926a). Some authors included a further 2 mountain voles in *argentatus* which are now considered species in their own right: *semicanus* (Gromov & Polyakov 1977, Zhang et al. 1997) and *tuvinicus* (Gromov & Polyakov 1977, Gromov & Erbajeva 1995). Current scope largely follows Rossolimo & Pavlinov (1992). We extracted *parvidens* from the scope of *argentatus* which follows *Mt*-evidence in Bhatt (2020).

Distribution (Figure 55). Mountains of Central Asia in north-eastern Afghanistan, northern Pakistan, northern India, north-eastern Turkmenistan, eastern Uzbekistan, Tajikistan, Kyrgyzstan, south-eastern Kazakhstan, and north-western China (Xinjiang). The range therefore encompasses an estimated 494,785 km² of the mountain landscape of northern Karakoram, Pamirs, Tien Shan, and isolated peripherial mountains of the Pamiro-Alay system (Karatau in Kazakhstan, Kul'dzhuktau in Uzbekistan and Kugitang in Turkmenistan). Typical habitats are accumulations of rocks and boulders in the alpine, sub-alpine and forest zones between 800 m and 4,830 m a.s.l. Altitudinal range in different mountain ranges is 800–2,800 m on Dzungarskiy Alatau, 850–2,800 m on Tarbagatay and Saur, 900–1,950 m on Kuldzuktau, 1,100–1,350 m on Karatau, 1,150–3,850 m on Tien Shan, 1,200–2,450 m on Kugitang, 1,350–4,100 m on Altai and Hissar, and 1,700–4,830 m on Karakorum. Along the southern and eastern edges of its distributional range the silver mountain vole is sympatric with *stoliczkanus* (see under that species); in Kazakhstan it is marginally sympatric with *strelzovi*. Putative sympatry with other mountain voles (*roylei*, *montosus)* requires verification.

Characteristics. *Alticola argentatus* is unique among arvicolines in having inner cheek pouches (length=12.7–35.9 mm, width=4.9–14.7 mm) capable

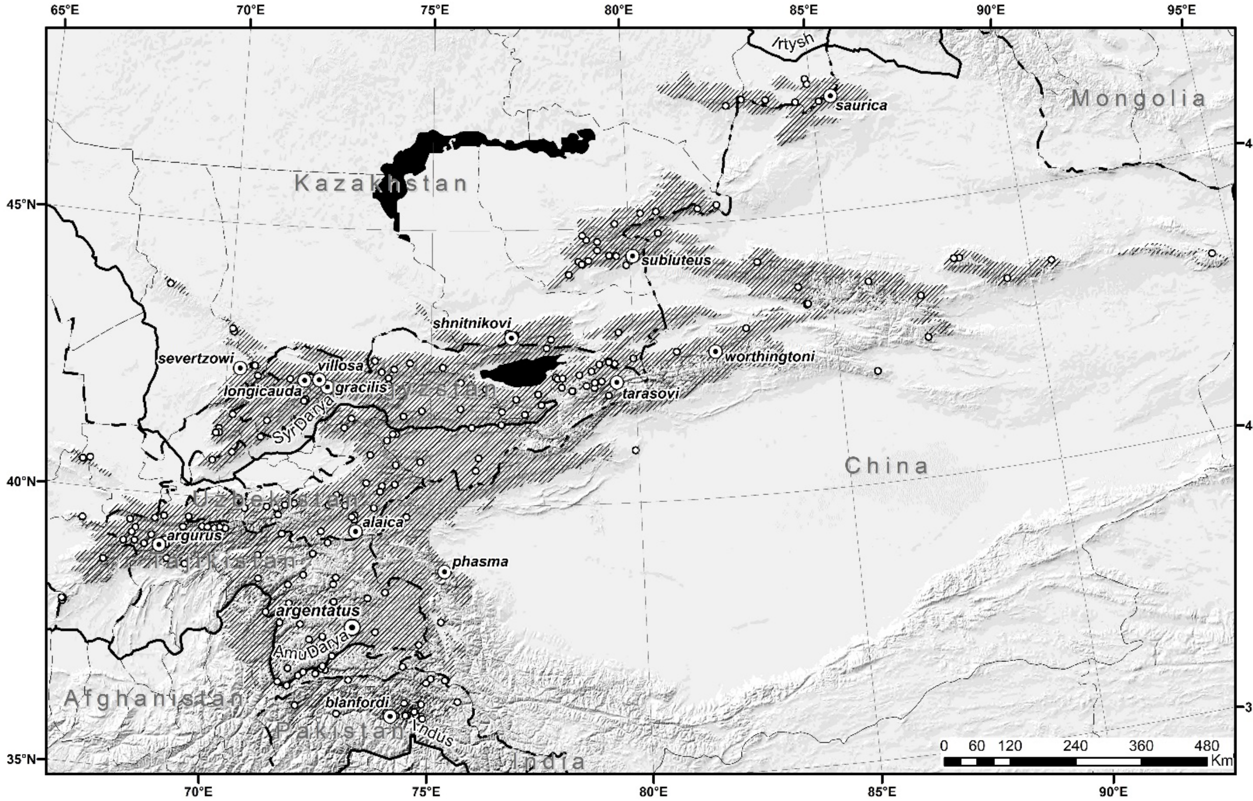


Figure 55: Distributional range of the silver mountain vole *Alticola argentatus*.

of carrying up to 5 g of food. Pouches were found in 28.2% of individual voles from Osh, Kyrgyzstan (Tarasovskaya 1993). External appearance, body proportions, skull morphology and dental pattern are highly variable. Size is small to medium and the tail is short to moderately long (TL/H&B=0.25–0.51, usually 0.37–0.44), slender, thinly haired and lightly pencilled (Figure 48c); length of pencil is 5–7.5 mm. Fur is soft (length=7–14 mm), either sandy fawn, light yellowish-grey, light grey-brown stained ochraceous buff or hair-brown with rusty cast above. Underside is pure white to light-grey, invariably shaded by slate hair bases and occasionally tipped with ochraceous-buff. Demarcation is usually faint, rarely distinct but never sharp. Tail is white and lightly dyed cream-buff; either uniform or bi-coloured (dorsal tail resembles the back). Feet are pure white or with a slight buff tint.

Skull shows no peculiarities (Figure 56). Braincase is usually long and the orbit is short. Dorsal profile is flat in adults. Auditory bullae vary in size from large and globular to rather small. Cheek-teeth are small, light and short (MxT/CbL=0.22–0.25). M^3 typically has 3 inner and outer salient angles, respectively; posterior lobe is short to moderately long (41–55% of the length of M^3; Rossolimo & Pavlinov 1992), in some populations showing traces of the 4th and 5th outer and the 4th inner salient angles (Figure 57a).

Karyotype is known in two subspecies (*argentatus* and *severtzowi*); diploid number is stable (2n=56) but the fundamental number varies (NF=58–62; Dimitriev 1990, Stubbe et al. 1994). Heterosomes are acrocentric: the X is large and the Y is a medium-sized element (Hielscher et al. 1992).

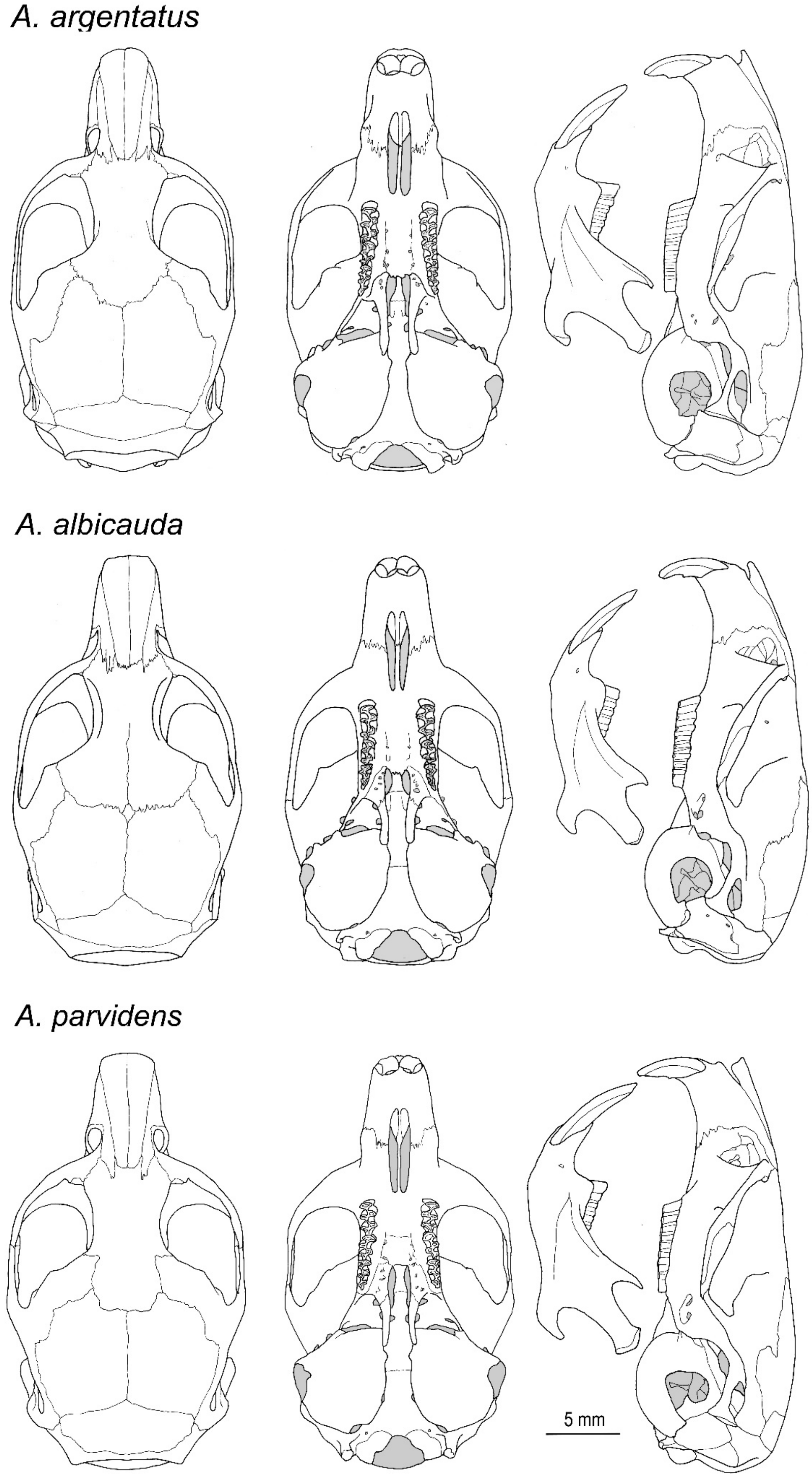


Figure 56: Skull in mountain voles: top–*Alticola argentatus* (Nookatskyi, Osh District, Kyrgyzstan); middle–*A. albicauda* (Liligo, Paju, Broad Peak, Pakistan); bottom–*A. parvidens* (Pandja near Kachu, Panjshir, Afghanistan).

Variation and subspecies. Revisions of subspecies resulted in very different numbers of taxa; e.g. Gromov & Erbajeva (1995) list 3 subspecies for Central Asia while Kuznetsov (1948a) recognised 5 subspecies in Kyrgyzstan alone. Differences among populations are reported over a small geographic distance, even along the elevational gradient; e.g. silver mountain voles are on average heavier at lower altitudes (Sludskiy et al. 1978). Below we summarise, with some modifications, subspecies recognised by Rossolimo (1989a) and Rossolimo & Pavlinov (1992); both sources based their conclusions upon an examination of specimens.

Alticola argentatus argentatus (Severtzov, 1879)

Arvicola argentata Severtzov, 1879:63. Type locality: "Alichur"; Latin transcription (p. 64) reads "Pamir–Alitschur"; i.e. Alichur, Pamir Mts., Murgabskiy raion, Gorniy Badakhshan Autonomous Province, Tajikistan (Baranova & Gromov 2003:61).

Synonyms. *Microtus (Alticola) argurus* Thomas, 1909; *Alticola argentata alaica* Rosanov, 1935; *Alticola argentata rosanovi* Ognev, 1940.

Taxonomy. The sole member of the Badakhshan group of subspecies (sensu Rossolimo & Pavlinov 1992).

Distribution. Pamir Mts. in Tajikistan, southern Kyrgyzstan (Alai ridge) and China (Tashkurgan in western Xinjiang); also Hissar Range (western Tajikistan and eastern Uzbekistan), Kuldzhiktau Mts. (Uzbekistan), and Kugitang ridge (eastern Turkmenistan).

Characteristics. Dimensions: BWt=20–44 g, H&B=100–120 mm, TL=43–59 mm, HF=18–22 mm, EL=14.2–22 mm, CbL=24.7–28.3 mm, ZgW=13.8–15.9 mm, MxT=5.4–5.7 mm. Tail is relatively long (TL/H&B=0.44–0.48), thinly haired and lightly pencilled (length of pencil ≈5 mm). Dorsal pelage is light brown, belly is greyish-white and demarcation line along the flanks is faint with a cream tint; tail is uniformly dirt white. Rostrum is long (=29–32% CbL), interorbital region is narrow, and braincase is wide (=46–49% CbL; Rossolimo & Pavlinov 1992); incisive foramina are slit-like, posteriorly nearly reaching the level of M^1 alveoli. M^3 is short relative to M^2; posterior loop is usually short and simple (Figure 58a).

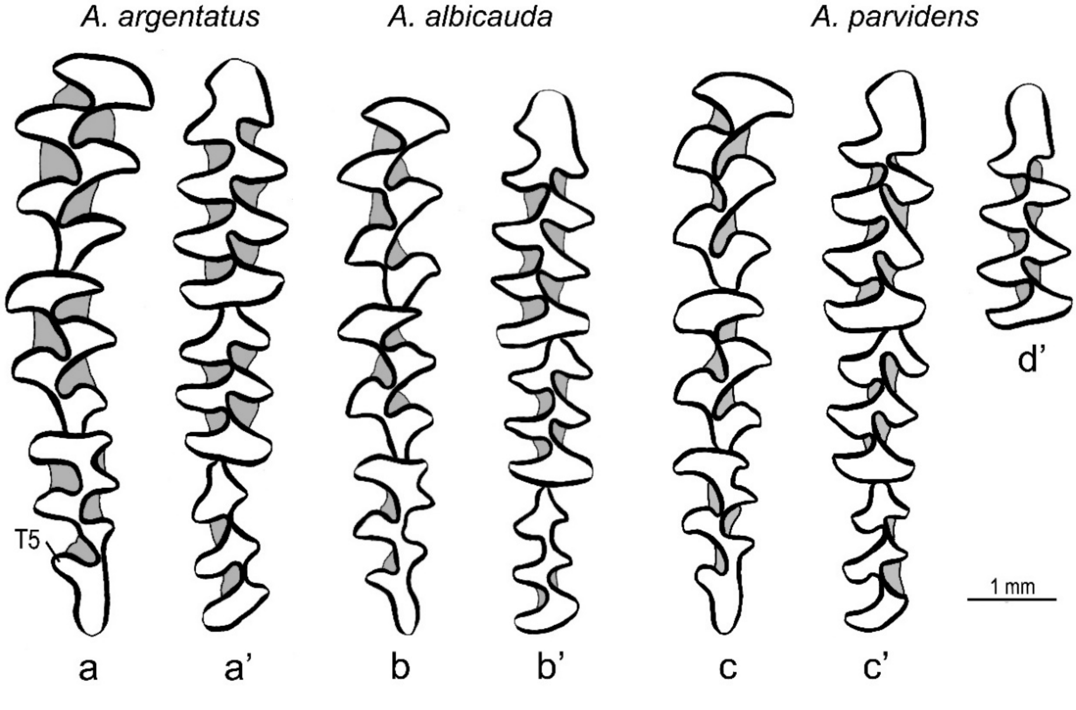


Figure 57: Molar pattern in mountain voles. *Alticola argentatus*: upper (a) and lower row (a'–Anzodskii pereval, Tajikistan); *A. albicauda*: upper (b) and lower row (b'–Phyang Nullah Lake Kashmir, India); *A. pavidens*: upper (c) and lower row (c'–Salang Pass, Parwan District, Afghanistan); isolated M_1 (d'–Do-Schank, Kinjantal, Hindu Kush, Afghanistan).

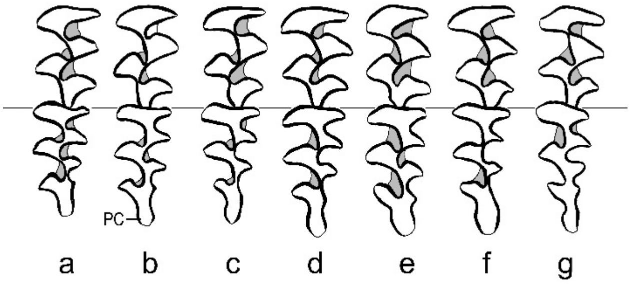


Figure 58: Morphology of 3rd upper molar in subspecies of *Alticola argentatus:* a–*A. a. argentatus* from Hissar Mts., Uzbekistan; b–*A. a. blanfordi* from Kashmir, India; c–*A. a. severtzowi* from Terskey Ala-Too, Kyrgyzstan; d–*A. a. worthingtoni* from Tekes Basin, Tian Shan, China; e–*A. a. phasma* from eastern Karakorum Mts., Xinjang, China; f—*A. a. subluteus* from the Almati region, Kazakhstan; g–*A. a. tarasovi* from the Inylchek River, eastern Kyrgyzstan. The length of M^2 is adjusted to a unit to emphasise the differences in the relative size of M^3.

Alticola argentatus blanfordi (Scully, 1880)

Arvicola blanfordi Scully, 1880:399. Type locality: "Gilgit, Kashmir", India. As shown by Bhatt (2020), Gilgit is inhabited by two Mt-clades of mountain voles which necessitates an unambiguous definition of the type locality of *blanfordi*. We restrict the type locality to "Nultar valley, near Gilgit, at elevations from 9000 to 10,000 feet [2,745–3,050 m]", which is the only locality mentioned by Scully (1881:207). Thomas (1918:371) designated BMNH voucher 8.3.9.17 as the lectotype; lectotype was seen.

Taxonomy. In the past, *blanfordi* was classified as a species in its own right (Hinton 1926a, Agrawal 2000) or a subspecies of *A. roylei* (Ellerman & Morrison-Scott 1951, Ellerman 1961), always with the inclusion of *lahulius* (here a synonym of *roylei*). Ascribed to the Hindu Kush group of subspecies (Rossolimo & Pavlinov 1992).

Distribution. The southern edge of the species' geographic range in northern India (Jammu and Kashmir) and northern Pakistan (southern Gilgit-Baltistan).

Characteristics. Dimensions: BWt=18–28 g, H&B=97–118 mm, TL=36–52 mm, HF=18–19 mm, EL=14–17.8 mm, CbL=24.1–26.5 mm, ZgW=13.2–14.7 mm, MxT=5.5–6.4 mm. Tail short to moderately long (TL/H&B=0.34–0.45); length of apical pencil ≈5 mm. Dorsal fur pale brown with a slight rufous hue, belly greyish white; hairs are isabelline at the meeting point along flanks of brown dorsal and white ventral fur. Feet white, tail dirt white with a medial dusky line. Skull shallow with a narrow interorbital region (≈15% skull length); bullae of moderate size; incisive foramina short, not reaching the level of M^1 alveoli. M^3 relatively long with moderately expanded posterior loop (Figure 58b).

Alticola argentatus severtzowi (Tikhomirov & Korchagin, 1889)

[Arvicola] severtzowi Tikhomirov & Korchagin, 1889:28. New name for *leucura* Severtzov.

Synonyms. *Arvicola Leucura* Severtsov, 1873 [preoccupied by *Arvicola leucurus* Gerbe, 1852]; *Alticola gracilis* Kashkarov, 1923; *Alticola longicauda* Kashkarov, 1923; *Alticola villosa* Kashkarov, 1923 [status uncertain]; *Alticola argentata shnitnikovi* Ognev, 1940.

Taxonomy. In the past frequently reported as *leucurus* which is a preoccupied name. Population from Terskey Alatau is transitional to *tarasovi*. Ascribed to Tien Shan group of subspecies (Rossolimo & Pavlinov 1992).

Distribution. Western, central and northern Tien Shan in Kazakhstan and Kyrgyzstan; also Karatau ridge in southern Kazakhstan.

Characteristics. Dimensions: BWt=19–38.5 g, H&B=86–116 mm, TL=32–49 mm, HF=16–20 mm, EL=12–18 mm, CbL=23.2–26.6 mm, ZgW=13.4–15.5 mm, MxT=5.6–6 mm. Tail short to moderately long (TL/H&B=0.33–0.40) and thinly haired; pencil is 7.5 mm long. Dorsal fur is very light brown to light drab, belly is greyish-white and demarcation line along the flanks is rather distinct; tail is uniformly dirt white or indistinctly bi-coloured. Braincase is short and narrow. Incisive foramina short (posteriorly not reaching the level of M^1 alveoli) and oval. M^3 is moderately long relative to M^2; posterior loop is moderately long (Figure 58c).

Alticola argentatus worthingtoni Miller, 1906

Alticola worthingtoni Miller, 1906:372. Type locality: "Tian Shan [Tien Shan] Mountains (Koksu), altitude 9000 feet [2,745 m]"; interpreted as "River Koksu in the Basin of Tekes, China" (Pavlinov & Rossolimo 1987:176).

Taxonomy. Hinton (1926a) endorsed *worthingtoni* to full species with 2 subspecies (the nominal and *subluteus*); synonymised with *roylei* in Ellerman & Morrison-Scott (1951). Ascribed to the Tien Shan group of subspecies (Rossolimo & Pavlinov 1992).

Distribution. Known only from the type locality (Luo et al. 2000).

Characteristics. Dimensions: CbL=25–26.8 mm, ZgW=14.7–15.2 mm, MxT=5.5–5.6 mm. Tail short (TL/H&B≈0.33); pelage light: dorsal side is smoke grey with a faint suffusion of pale ochraceous buff, speckled with black hair tips; belly white; feet white with a faint creamy tint. M^3 is long relative to M^2, posterior loop long (Figure 58d).

Alticola argentatus phasma Miller, 1912

Alticola phasma Miller, 1912b:5. Type locality: "eastern side of Kara Korum [Karakoram] Mts., Chinese Turkestan, at altitude of between 9000 and 10,000 feet [2,745–3,050 m]", China.

Taxonomy. Hinton (1926a) endorsed *phasma* as a species in its own right; subsequently synonymised with *roylei* (Ellerman & Morrison-Scott 1951). Ascribed to the Tien Shan group of subspecies (Rossolimo & Pavlinov 1992).

Distribution. Eastern Karakorum, Xinjiang, China (Luo et al. 2000).

Characteristics. Dimensions: H&B=101 mm, TL=38–41 mm, HF=19.5–20 mm, EL=16 mm, CbL=26.8–27 mm, ZgW=14.8–15 mm, MxT=6.2–6.4 mm. Tail relatively short (TL/H&B=0.37–0.40); dorsal pelage pallid smoke grey, belly pure white, legs and tail white. Skull is relatively narrow (ZgW/CbL≈0.55), incisive foramina protrude behind the level of M^1 alveoli; bullae are of moderate size. M^3 visibly longer than M^2, posterior loop short (Figure 58e).

Alticola argentatus subluteus Thomas, 1914

Alticola worthingtoni subluteus Thomas, 1914b:570. Type locality: "In a canyon Tischkan", Panfilov District, Almaty Region, Kazakhstan.
Synonyms. *Alticola argentata saurica* Afanasiev & Bazhanov, 1948.

Taxonomy. Classified in the past as a subspecies of *A. worthingtoni* (Hinton 1926a) or *A. roylei* (Ellerman & Morrison-Scott 1951). Ascribed to the Tien Shan group of subspecies (Rossolimo & Pavlinov 1992).

Distribution. The extreme north-eastern Tien Shan (i.e. Tarbagatai, Saur and Dzungarian Alatau) in eastern Kazakhstan (Rossolimo & Pavlinov 1992) and northern Xinjiang in China (Luo et 2000).

Characteristics. Size large: BWt=31.5–45 g, H&B=108–126 mm, TL=31–52 mm, HF=17–20 mm, EL=14–17 mm, CbL=26.5 mm, MxT=5.7 mm. Tail is moderately long (TL/H&B=0.37–0.39); pelage is light, smoke grey with a faint suffusion of pale ochraceous buff, speckled with black hair tips dorsally; belly white, shaded pale pinkish buff; feet and tail white with a slight buffy tinge. M^3 long relative to M^2, posterior loop long (Figure 58f).

Alticola argentatus tarasovi Rossolimo & Pavlinov, 1992

A[lticola] a[rgentatus] tarasovi Rossolimo & Pavlinov, 1992:165. Type locality: "Banks of Inylchek River, system of Inylchek and Sary Ridges, E[astern] Kirghizia [Kyrgyzstan]".

Taxonomy. Ascribed to the Tien Shan group of subspecies (Rossolimo & Pavlinov 1992).

Distribution. Southern Tien Shan (Aksay, Atbashi and Sarydzhaz) in southern Kyrgyzstan and Xinjiang (China).

Characteristics. Size moderate: BWt=26–37 g, H&B=97–119 mm, TL=34–41 mm, HF=16–18 mm, EL=11–17 mm, CbL=24.1–27.1 mm, ZgW=14–14.9 mm, MxT=6–6.6 mm; tail is rather short (TL/H&B=0.33–0.37). Colour as in the nominotypical subspecies: back is cloudy pale rusty with brown suffusion; tail entirely white. Braincase narrow, interorbital constriction wide, bullae short and wide; incisive foramina short, posteriorly not reaching the level of M^1 alveoli. M^3 long relative to M^2, posterior loop long and complex (Figure 58g).

Alticola albicauda (True, 1894) – White-tailed Mountain Vole

Arvicola albicauda True, 1894:12. Type locality: "Braldu Valley, Baltistan", Kashmir, India.

Synonyms. *Alticola glacialis* Miller, 1913; *Alticola acmæus* Schwarz, 1939.

Taxonomy. A species in its own right in Hinton (1926a) and subsequently synonymised with *roylei* (Ellerman 1941, 1961). In phylogenetic trees *A. albicauda* nests inside *A. argentatus* (see section on *A. argentatus*) as a sister species to *parvidens* (Bhatt 2020). Miller's *glacialis* was considered a species in its own right (Hinton 1926a) or a subspecies of either *roylei* (Ellerman & Morrison-Scott 1951, Ellerman 1961) or *argentatus* (Rossolimo & Pavlinov 1992, Pardiñas et al. 2017). Morphologically, *glacialis* is an outlier in *argentatus* but closely resembles *albicauda*; moreover, its type locality is inside the range of *albicauda*.

Distribution (Figure 59). The range covers 19,575 km^2 in north-eastern Pakistan (Northern Areas), northern India (Jammu and Kashmir), and the Pamir Plateau in Tashikuergan County (Xinjiang, China; Liu et al. 2020). Nearly all records are on the left bank of the Indus River, while *A. montosus* occurs on the opposite bank.

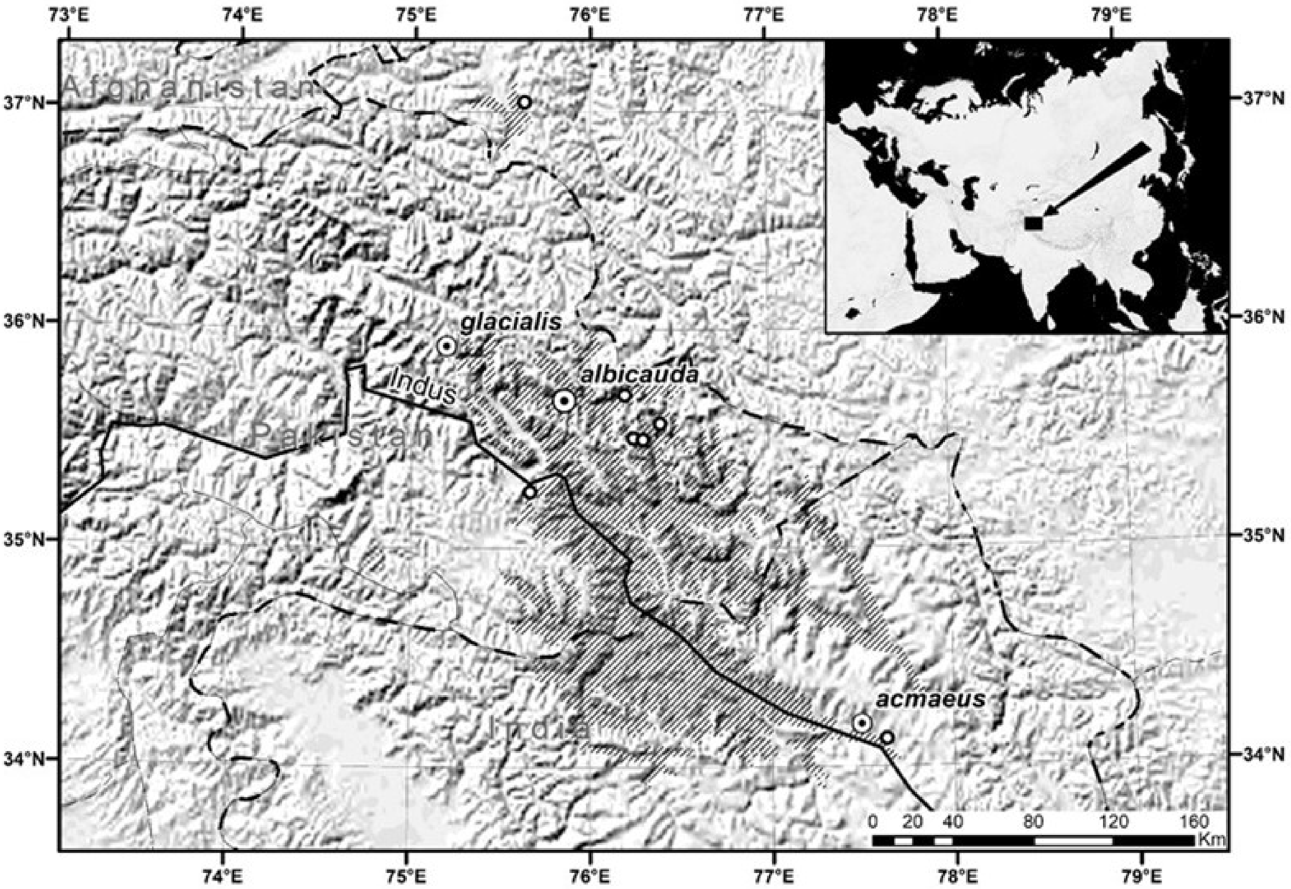


Figure 59: Distributional range of the white-tailed mountain vole *Alticola albicauda*.

The species occupies accumulations of rocks from 3,440 m (the type) to 4,050 m a.s.l. (Ghanche, Dalsangpa).

Description. A moderately large and short–tailed (TL/H&B=0.25–0.34) mountain vole. Dimensions: H&B=101–108 mm, TL=28–32 mm, HF=21–22 mm, CbL=24.8–26.4 mm, ZgW=13.7–15 mm, MxT=5.9–6.5 mm. Pelage is soft (hairs up to 15 mm long), light reddish gray to dull yellowish grey dorsally; underside is pure white, pallid-mouse-grey, or grey, demarcation obvious. Juveniles are mouse-grey with brown wash. Feet are white; tail is white or light gray throughout, densely clad with stiff hairs, well-tufted and with a long pencil (=10–12 mm); annulation is not entirely concealed by hairs (Figure 48b). Skull is lightly built with no ridges; squamosal processes are feeble; interorbital constriction is wide, braincase is large, and incisive foramina short (not reaching M^1 alveoli). The skull is deep (height behind M^3=32–34% CbL) and braincase is large (Figure 56); interorbital constriction is wide. Zygomatic arches moderately expanded (ZgW/CbL=0.54–0.57); mandible is shallow. Molars essentially as in *A. roylei;* maxillary tooth-row is short (MxT/CbL=0.24–0.25); M^3 short relative to M^2 with a short heel; M_1 with 4 closed and alternating triangles, T5 opens in anterior lobe (Figure 57b).

Variation and subspecies. Monotypic species.

Alticola parvidens Schlitter & Setzer, 1973 – Hindu Kush Mountain Vole

Alticola roylei parvidens Schlitter & Setzer, 1973:165. Type locality: “20.5 mi [33 km] N[orth of] Dir, 10,400 ft. [3,200 m], Dir State, West Pakistan”.

Taxonomy. Described as a subspecies of *roylei* and subsequently allocated to the Hindu Kush subspecies group of *argentatus* (Rossolimo & Pavlinov 1992). Bhatt (2020) demonstrated a sister relationship between the Hushe Valley clade (i.e. *albicauda*) and the Hindu Kush clade (*parvidens*) of mountain voles. The lineages diverged at 0.6 Ma (CI=0.33–1.14 Ma; Bhatt 2020) and differ morphologically, hence we treat them as a distinct species.

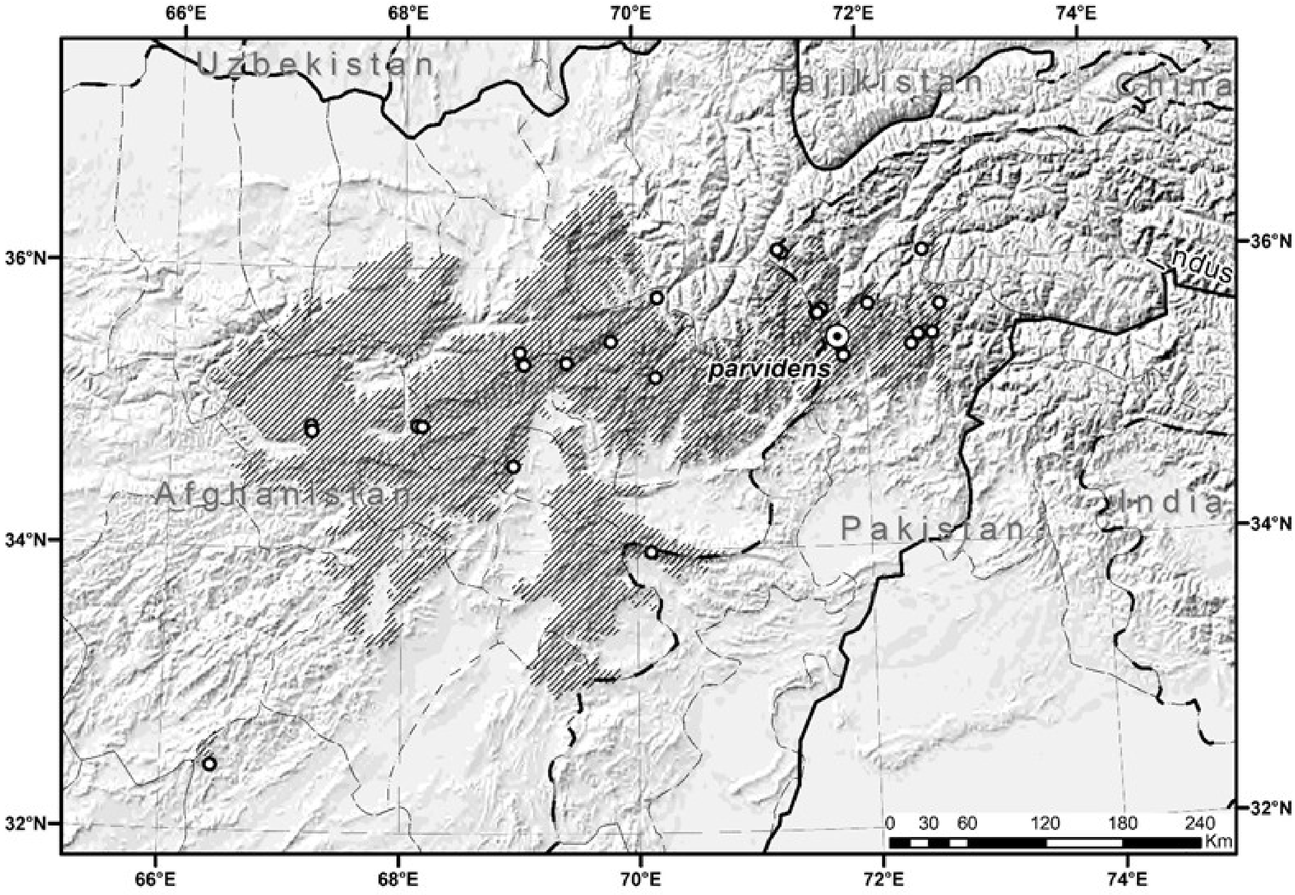


Figure 60: Distributional range of the Hindu Kush mountain vole *Alticola parvidens*.

Distribution (Figure 60). Endemic to the Hindu Kush Mountain Range in C Afghanistan (Provinces of Baghlan, Bamiyan, Kabul, Nurestan, Panjshir, Parwan, and Zabol) and adjacent north-western Pakistan (North-West Frontier and Federally Administered Tribal Areas). The area is estimated at 85,285 km^2. Habitat is as in *argentatus* with an elevational range of 2,150–3,850 m.

Characteristics. Dimensions: BWt=22–44 g, H&B=92–125 mm, TL=40–59 mm, HF=18–21 mm, EL=13–18 mm, CbL=25.7–28.1 mm, ZgW=13.9–15.9 mm, MxT=5.8–6.8 mm. Similar to *argentatus*; size is medium and tail is proportionally long (TL/H&B=0.39–0.54). Fur is soft, brown with a red-brown shade. Underside is pure white to light-grey, heavily shaded by slate hair bases and occasionally shaded buffy; demarcation on flanks is faint to distinct. The tail is thinly to densely haired, either bi- coloured (brown above, buffy-white below) or light-grey on all sides. Feet are pure white or with a slight buff tint; ears are grey. The skull is lower than in *albicuada* (height behind $M^3 \approx 31\%$ CbL), braincase is shorter and zygomatic arches are slightly more expanded (ZgW/CbL=0.54–0.58). Auditory bullae are small and globular; hard palate is shorter than incisive foramina (longer in *albicauda*); mandible is shallow. Cheek-teeth are small, light and short (MxT/CbL=0.23–0.26) and their enamel pattern is like in *albicauda*. Karyotype is not known.

Variation and subspecies. Monotypic species.

Species group *stoliczkanus*

Alticola stoliczkanus (Blanford, 1875) – Stoliczka's Mountain Vole

Taxonomy. Hinton (1926a) split *A. stoliczkanus* into 4 species (*stoliczkanus, stracheyi, acrophilus,* and *lama*), and Ellerman (1941) recognised an additional species (*kaznakovi*). The number of species was subsequently reduced to 2 (*stoliczkanus* and *stracheyi*; Heptner & Rossolimo 1968, Mitchell 1975, Honacki et al. 1982), or to a single one (Ellerman 1947, 1961). Chinese (Zhang et al. 1997, Luo et al. 2000, Wang 2003) and Indian

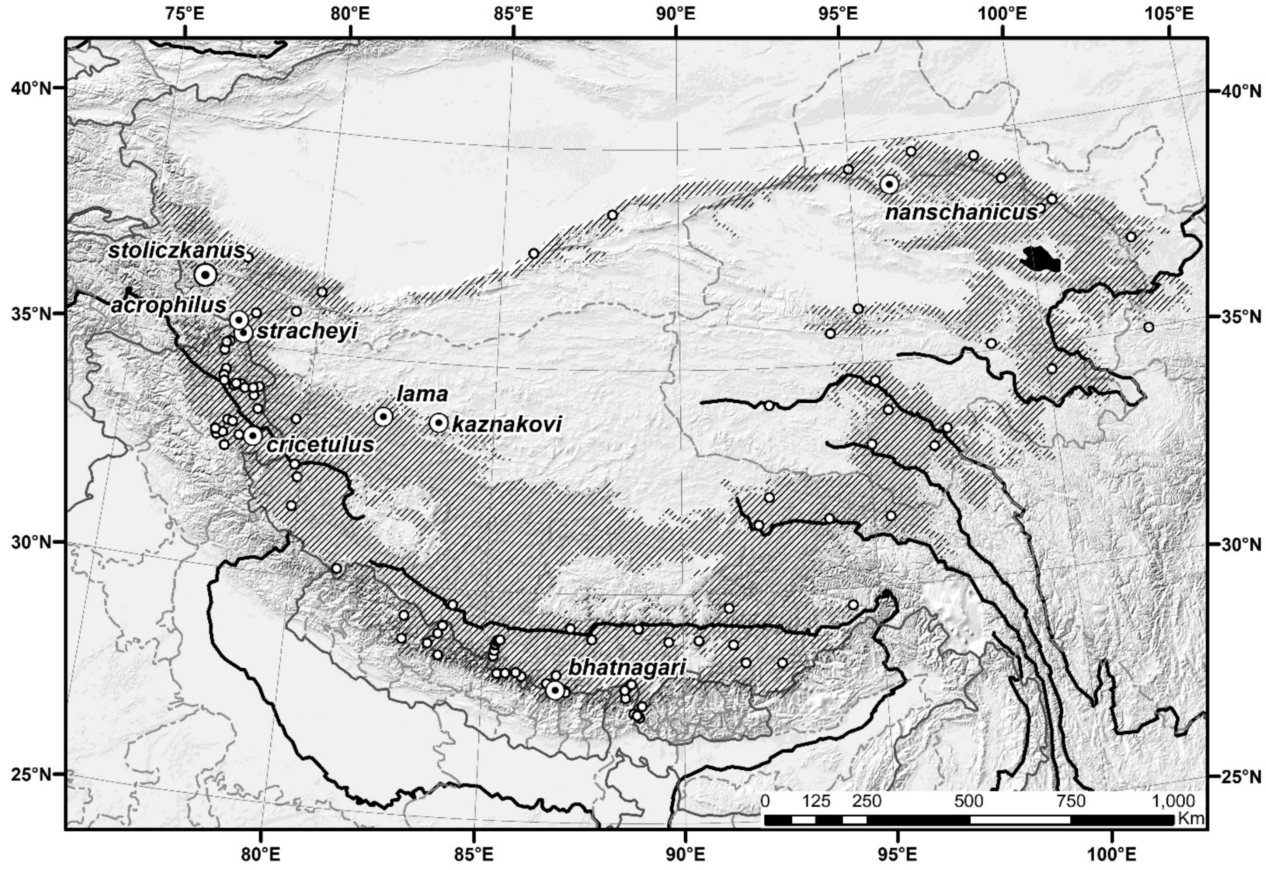


Figure 61: Distributional range of the Stoliczka mountain vole *Alticola stoliczkanus*.

authors (Agrawal 2000, Alfred et al. 2002) continue treating *stoliczkanus* and *stracheyi* as distinct and partly sympatric species (Xia et al. 2003). In Qomolangama, Tibet, they reportedly segregated along the elevational gradient with *stracheyi* occupying lower elevations (3,340–4,200 m) and *stolickanus* inhabiting higher altitudes (4,200–5,100 m; Hu et al. 2014). Luo et al. (2000) used the bullae size (inflated in *stoliczkanus*) to distinguish between these two voles. Molecular evidence disproved the status of independent species for *stracheyi* (Tang et al. 2018).

In the past, *A. barakshin* was frequently regarded as conspecific with *A. stoliczkanus* (see under that species).

Distribution (Figure 61). High mountain ridges and plateaus of Tibet and the Himalayas, from Karakorum, Hindu Kush and Kashmir (Pakistan and India), to western Gansu in the east, and from southern Kunlun Mts. (Xinjiang) to northern Nepal, Sikkim and possibly Bhutan. The range of the species encircles high mountain ridges surrounding the Tibet Plateau and Qaidam Basin. The species is absent from extensive regions of East Tibet (Kham) and Far East Tibet (Amdo). Details of the western distributional border in Xinjiang are poorly resolved, hence it is not known how closely the range approaches Tajikistan and Kyrgyzstan where the species has not been recorded (Shenbrot & Krasnov 2005). The geographic range of *A. stoliczkanus* is by far the largest of any mountain vole, covering 1,099,440 km^2. The vole occupies rocky habitats (moraines, boulders) above the timber line where *A. stoliczkanus* is usually the only rodent species (e.g. Daniel & Hanzák 1985). Vertical distribution is contiguous between 3,900–5,450 m, although these voles may descend as low as 1,760 m and occupy isolated mountain peaks encircled by glaciers (nunataks) up to 6,140 m *(*Daniel 2015). In the north-central edge of its range (Qilian Mts.), *A. stoliczkanus* was recorded at elevations of 3,600–3,900 m (Li et al. 2003); vertical range in Tibet proper is 3,340–5,100 m (Hu et al. 2014). Sympatry was reported with *argentatus* and *albicauda* (Rossolimo & Pavlinov 1992) in Kashmir; in Nepal *A. stoliczkanus* was found in sympatry with *A. roylei* (Kryštufek et al. 2017).

Characteristics. Small- to medium-sized mountain vole with a short tail and simplified M^3 occlusal pattern. Tail is approximately the same length as the hind foot (TL/H&B=0.13–0.22), densely clothed with stiff white, cream or dirty-white hairs which completely hide the annulations (Figure 48d); the terminal pencil is distinct (length=8.5–9.5 mm). Ears are rounded, covered by hair along the outer edge and only slightly protruding above the fur. Feet are small, white, dirty-white or cream; palms and soles have few short hairs between the digital pads but are densely haired behind; claws are long, sharply pointed and compressed and are hidden by long hairs. The front thumb is vestigial bearing a minute nail (reported as clawless in Blanford 1879). Toes are short and blunt; interdigital plantar pads are of approximately the same size as the medial metatarsal pad (Figure 49b). Pelage (length up to 15 mm) is dense, soft and occasionally woolly. Back is pale yellowish-brown, pinkish-buff or bright rusty brown (ferruginous), inconspicuously clouded by slate hair bases and interspersed with longer dark brown hairs. Belly and upper lips are pure white and frequently sharply contrast the upper surface; hair bases are slate. Immature specimens are darker and greyer, and their tail is bi-coloured. Proximal baculum (Figure 62) is a simple straight rod, 1.9 mm long and 0.7 mm wide across the basal expansion (Gregori & Petrov 1976).

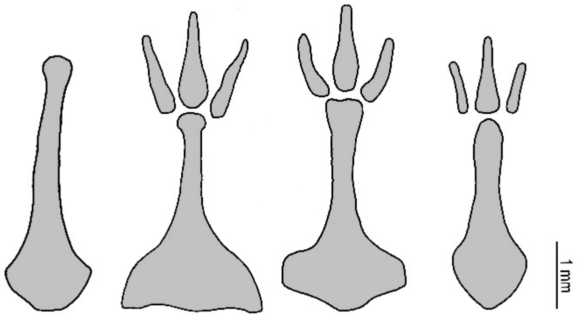


Figure 62: Baculum in mountain voles *Alticola*: a–*A. stoliczkanus* (Mt. Makalu, Nepal); b–*A. strelzovi* (Kosh-Agach, Altai Republic, Russia); c–*A. macrotis* (Kosh-Agach district, Altai Republic, Russia); d–*A. lemminus* (Lake Grand, Magadan, Russia).

Skull is rather deep (height behind M^3=30.5–34.5% CbL) and angular for mountain voles with weak temporal ridges and modest squamosal processes. Zygomatic arches are moderately expanded (ZgW/CbL=0.52–0.60). Orbit is long (~⅓ CbL), braincase is short (~½ CbL), nearly square-shaped, and rostrum is long and slender. Incisive foramina are short, not protruding behind the line of M^1 alveoli (Figure 63). *A. stoliczkanus* has the most reduced M^3 among mountain voles (Figure 64b,c). The tooth is short and of simplified structure: (i) width of anterior lobe is ~½ the total length of the molar; (ii) the two labial triangles (T2 and T4) tend towards reduction and are nearly absent in some individuals; T4 opens widely into the posterior lobe; (iii) the lingual side usually has only 2 salient angles; the 3rd angle (T5) is rarely developed.

Variation and subspecies. Mead & Nadachowski (1999) tentatively recognised 6 subspecies (*acrophilus, kaznakovi, lama, nanschanicus, stoliczkanus, stracheyi*) and all but *stracheyi* were known from a single locality. Revision by Rossolimo & Pavlinov (1992) resulted in 3 weakly defined subspecies of unresolved geographic borders. These results are followed below with some modifications resulting from our study of museum specimens. Colour is too variable to be of much significance in diagnosing groups of populations.

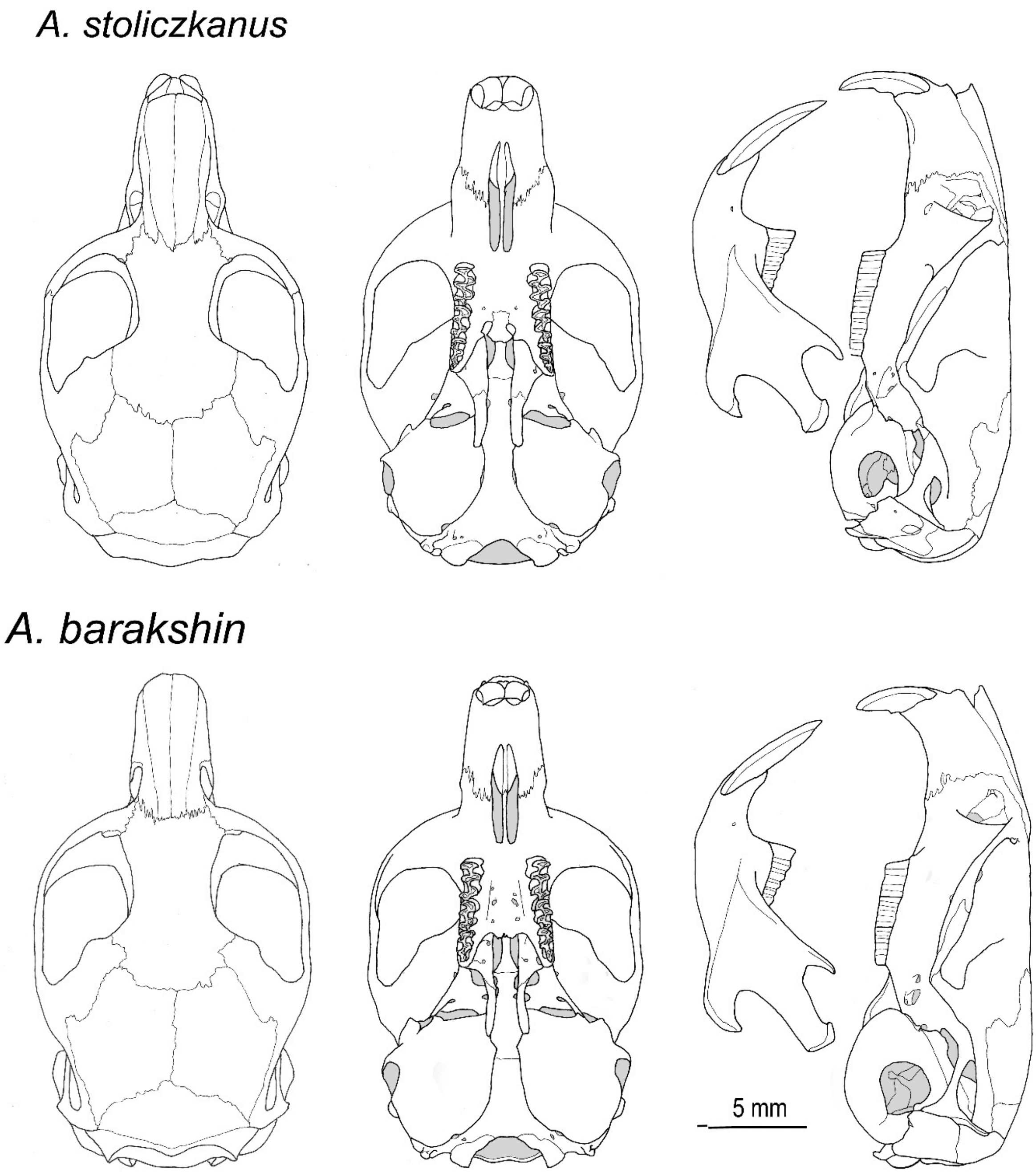


Figure 63: Skull in mountain voles: top–*A. stoliczkanus* (Mesokantu hágó, Nepal): bottom–*A. barakshin* (Bodonchiyn-Göl, Altai Mts., Mongolia)

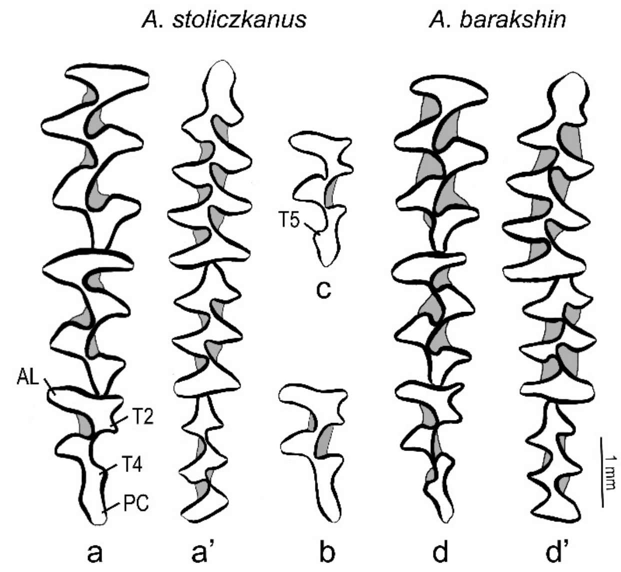


Figure 64:: Molar pattern in mountain voles. *Alticola stoliczkanus*: upper (a) and lower row (a'–Khumbu, Lobuche, Nepal); isolated M^3 of *Alticola stoliczkanus stoliczkanus* (b–Ladakh, India) and Alticola stoliczkanus lama (c–Shara-Gol, Gansu, China; topotype of nanschanicus). *Alticola barakshin*: upper (d) and lower row (d'– Tuva Region, Russian Federation).

Alticola stoliczkanus stoliczkanus (Blanford, 1875)

Arvicola stoliczkanus Blanford, 1875:107. Syntypes originate from two localities: "Nubra Valley, Ladák; [and] Aktágh near Karakoram Pass"; both sites are located in the "Kuenlun Mountains, Northern Ladak" (Hinton 1926a:321), India. Rossolimo & Pavlinov (1992:172) designated the lectotype (Zoological Survey of India No. 15707) and therefore restricted the type locality to "Nubra Valley, Ladakh".

Synonyms. *Arvicola stracheyi* Thomas, 1880; *Microtus cricetulus* Miller, 1899; *Microtus acrophilus* Miller, 1899.

Distribution. Karakorum, Hindu Kush and Kashmir in Pakistan and western India.

Characteristics. Medium to large: H&B=101–127 mm, TL=14–23 mm, HF=17–20 mm, EL=14–14.6 mm, CbL=24–28 mm, ZgW=14.6–16.4 mm, MxT=5.8–7 mm. Bullae large (longer than MxT); M^3 occasionally with 3 salient angles on the lingual side.

Alticola stoliczkanus lama (Barrett-Hamilton, 1900)

Microtus (Alticola) lama Barrett-Hamilton, 1900:196. Type locality: "25 miles [40km] south-east of Lake Arucho [Aru-cho], W[est] Tibet, altitude 16,000 ft. [4,875 m]", China.

Synonyms. *Microtus nanschanicus* Satunin, 1903; *Microtus kaznakovi* Satunin, 1903.

Taxonomy. Allen (1940) retained the rank of species for *nanschanics*.

Distribution. High mountain ridges surrounding the Tibetan Plateau and the Qaidan Basin from all sides, except the west.

Characteristics. Slightly larger than *bhatnagari:* BWt=25–50 g, H&B=90–121 mm, TL=15–27 mm, HF=17–20 mm, EL=11–16 mm, CbL=24.4–28.2 mm, ZgW=14.7–16.6 mm, MxT=5.8–6.8 mm. Bullae long; M^3 frequently with 3 salient angles on the lingual side.

Alticola stoliczkanus bhatnagari Biswas & Khajuria, 1955

Alticola bhatnagari Biswas & Khajuria, 1955:29. Type locality: "Mingbo (ca. 14,500 ft [4,420 m]), Langmoche Valley, Khumbu, Nepal".

Taxonomy. *A. bhatnagari* was originally described as a species in its own right. It was sometimes treated that way (e.g. Ellerman 1961) or was synonymised with *A. roylei* (Gromov & Polyakov 1977).

Distribution. Southern slopes of the Himalayas in Nepal and Sikkim.

Characteristics. Small to medium: BWt=21–38 g, H&B=93–114 mm, TL=13–25 mm, HF=16–19.9 mm, EL=9.5–13 mm, CbL=21.3–28.7 mm, ZgW=11.5–16.5 mm, MxT=5.4–6.5 mm. Bullae small (shorter than MxT); M^3 simplified, never has the 3rd inner salient angle; both labial salient angles (T2 and T4) conspicuously reduced in size.

Alticola barakshin Bannikov, 1947 – Gobi Altai Mountain Vole

Alticola barakshin Bannikov, 1947:217. Type locality: "Dzun Saykhan, Gurvan Saykhan Ridge, Govi Altai Mts.", Omnogovi, Mongolia.

Taxonomy. Although described as a species in its own right, in the past *A. barakshin* was regarded as conspecific with either *stoliczkanus* (Gromov & Polyakov 1977, Corbet 1978, Pavlinov & Rossolimo 1987), *roylei* (Heptner & Rossolimo 1968, Honacki et al. 1982), or *argentatus* (Sokolov & Orlov 1980). Full species status was restored on the grounds of morphology (Rossolimo 1989b) and confirmed using karyotype (Hielscher et al. 1992), allozymes (Hille & Stubbe 1996) and nucleotide sequences (Lebedev et al. 2007, Tang et al. 2018). Cross-breeding trials of *A. barakshin* with *semicanus* and *argentatus* failed to produce interspecific hybrids (Stubbe et al. 1994).

Distribution (Figure 65). The majority of the geographic range is in the Mongol Altai Mts. (in Bayan-Ölgii and Hovd) and the Gobi Altai Mts. of south-western Mongolia. The range encompasses the Mongun-Tayginskiy range (southern Tuva region in Russia), Barkol County (Dzungaria in China) and covers 125,680 km². *A. barakshin* is less dependent on rocky places than other mountain voles and frequently seeks shelter under shrubs (*Juniperus, Artemisia*). The majority of records are from juniper stands at 1,060–3,389 m a.s.l. At higher altitudes, *argentatus* and *strelzovi* replace *barakshin* and dominate the stony mountain steppe of NW Mongolian Altai (Bannikov 1954).

Characteristics. A short-tailed vole of modest size (Figure 67d), resembling *A. stoliczkanus* in external appearance and colouration. Dimensions: BWt=28.3–62.8 g, H&B=95–129 mm, TL=15–30 mm, HF=15–22 mm, EL=12.4–21 mm, CbL=25.8–28.9 mm, ZgW=14–16.4 mm, MxT=5.7–7 mm. Whiskers are long (≈39 mm). Tail (TL/H&B=0.14–0.25) is light sandy above, white below and densely clothed with stiff hairs; terminal pencil is 7–10 mm long (Figure 48g). Hair (length≈12 mm) is soft, brownish-grey above; rump, neck and flanks washed drab; demarcation on flanks is either sharp or faint. Belly is dirty-white, occasionally washed buff to rusty. Feet are white and clouded yellowish; ears grey and margined buff.

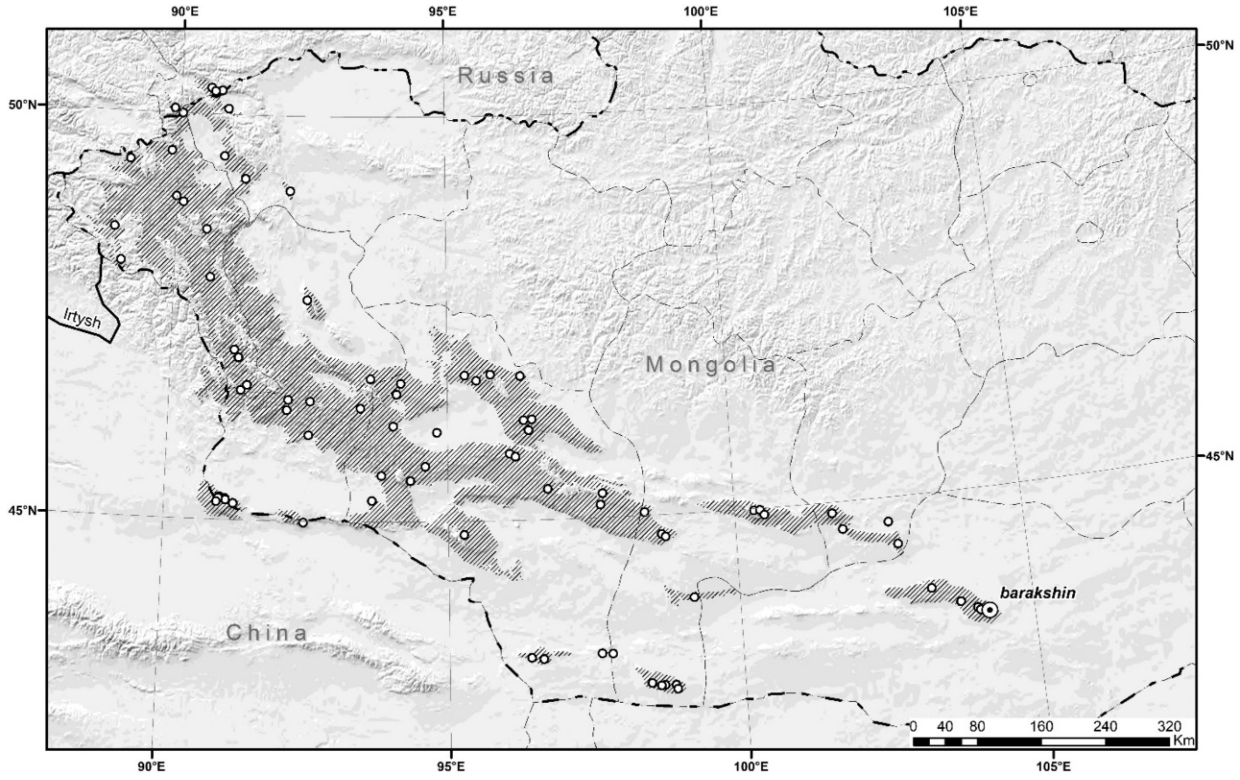


Figure 65: Distributional range of the Gobi Altai mountain vole *Alticola barakshin*.

The skull is robust and ridged (Figure 63) with supratemporal ridges 2 mm apart in the interorbital region. Dorsal profile depressed in the interorbital region. Braincase long (short in *stoliczkanus*) and moderately deep (height behind M^3 =29.8–31.3% CbL). Squamosal processes are prominent; incisive foramina short, not reaching the level of M^1 alveoli. Bullae large (length≈width) and of approximately the same length as the diastema (much shorter than diastema in *stoliczkanus*). Interparietal more robust than in *stoliczkanus*; sagittal diameter/transverse diameter≈0.5 (≈0.3 in *stoliczkanus*). M^3 laterally compressed, otherwise as in *stoliczkanus,* i.e. with 2 inner and 3 outer salient angles; the 3rd inner salient angle is present in ~⅓ of individuals. Posterior cap of M^3 is never pronouncedly elongated as commonly observed in *A. stoliczkanus bhatnagari* (cf. Fig. 6 in Heptner & Rossolimo 1968); length of PL/length of M^3≈0.43–0.57 (0.56–0.67 in *stoliczkanus*; Rossolimo 1989b).

Karyotype (2n=56) has a polymorphic 1st autosomal pair (subtelocentric or acrocentric), hence the fundamental number is variable (NF_a=58–62); the small autosomal pair is invariably bi-armed. The X chromosome is large acrocentric and the Y is small metacentric (Hielscher et al. 1992, Stubbe et al. 1994).

Variation and subspecies. A monotypic species (Rossolimo & Pavlinov 1992). In 5 geographic samples, length of skull ($\bar{x}$±SD) varied between 27.41±0.82 mm (northern Mongolian Altai) and 28.45±0.91 mm (Trans-Altai Gobi, Mongolia; Rossolimo 1989b).

Alticola strelzovi (Kastschenko, 1899) – Strelzov's Mountain Vole

Taxonomy. Throughout the 20th century, *strelzovi* was classified as the sole member of the subgenus *Platycranius*. Lebedev et al. (2007) showed that *Alticola* is paraphyletic with respect to *Platycranius*, hence *strelzovi* is classified here in the nominal subgenus of *Alticola*. The vast majority of authors treated *Platycranius* as monotypic, but Hinton (1926a) and Ellerman (1941) regarded *alliarius* Pallas as a species of *Platycranius,* however distinct from *strelzovi*.

The species name is frequently incorrectly spelled as *strelzowi*.

Distribution (Figure 66). Strelzov's mountain vole occupies the following major mountains in Central Asia: Kazakh Highlands, Tarbagatay, Altai, Mongolian Altai, and Tannu-Ola. The range covers a surface area of 330,310 km^2 and encompasses eastern Kazakhstan (Akmola, Karagandy, Pavlodar, and eastern Kazakhstan), Altai Republic and Tuva (Russian Federation), north-western Mongolia (Bayan-Ölgiy, Dzavhan, Khovd, and Uvs), and the northern Xinjiang (China). *Alticola strelzovi* occupies accumulations of rocks, isolated boulders and talus slopes (inclination=5–70^0) in steppes, semi–deserts and river

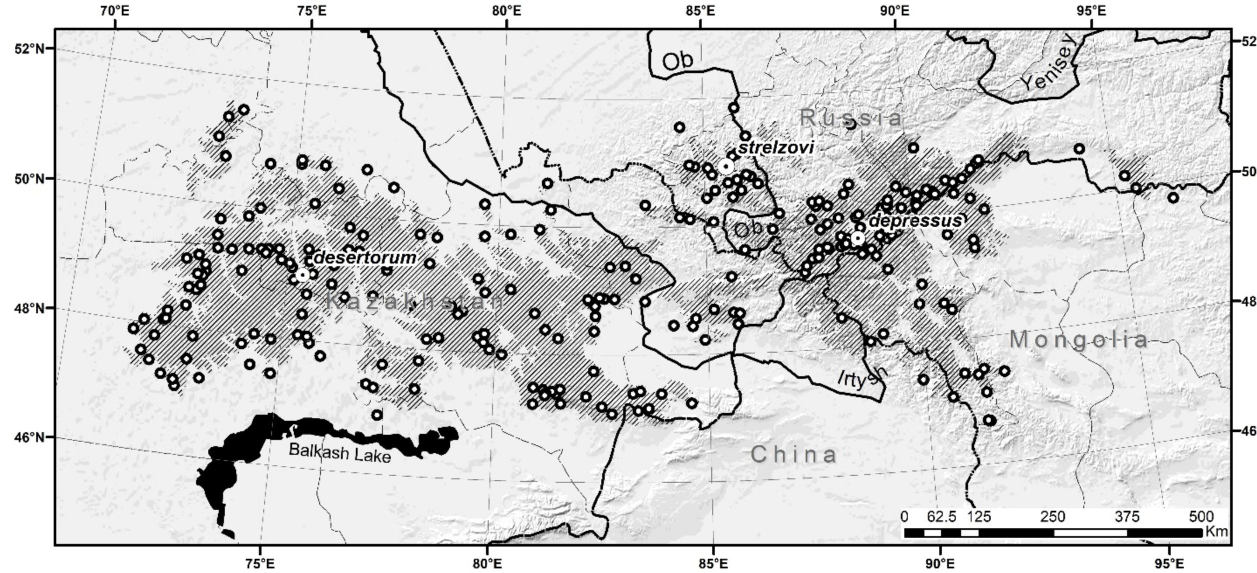


Figure 66: Distributional range of Strelzov's mountain vole *Alticola strelzovi*.

valleys. Habitat is fragmented at various spatial scales; e.g. in the Ermentau Mts. (Kazakhstan), the distance between suitable patches is 500–800 m (Sludskiy et al. 1978). Altitudinal range is between 280 m (Irtysh Valley near Semipalatinsk; Kazakhstan) and 3,150 m (Saylyugem on south-western Altai). This vole is sympatric with *A. macrotis*.

Characteristics. A large mountain vole with a moderately long (TL/H&B=0.21–0.44) and thick tail, large circular ears (Figure 67a,b), and long whiskers (44–51 mm). Fur is soft, dense (138 hairs/mm^2; Sludskiy et al. 1978) and long (10–13 mm). Dorsal side is light-drab, drab or cinnamon-drab, mouse-grey or ash-grey to wood-brown; fur is slightly darkened with scattered black-tipped hairs. Flanks are lighter and frequently more greyish, belly is light, whitish to greyish-white; demarcation line is either faint or obvious. Shoulders are lighter (cream or buff) and there is a buff subaricular tuft. Ears are hairy throughout, grey and margined buff;

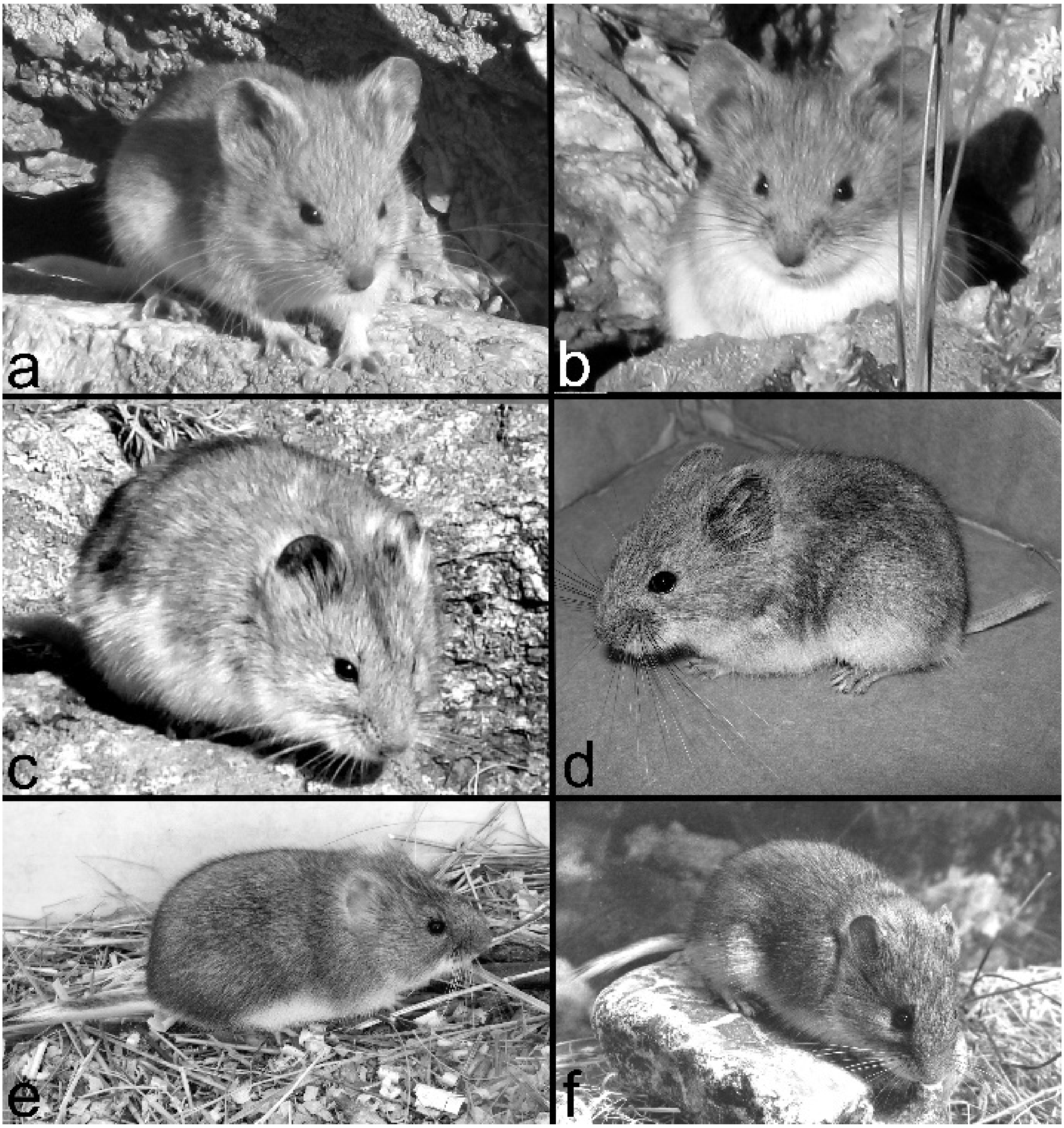


Figure 67: Mountain voles of the *stoliczkanus* species group: a,b–*Alticola strelzovi*; c–*A. semicanus*; d–*A. barakshin*; e–*A. tuvinicus*; f–*A. olchonensis*. *A. semicanus* is from Central Mongolia and the remaining individuals originate from the Russian Federation. Photo courtesy: Yuriy N. Litvinov (a,b), Nataliya V. Lopatina (d,e,f) and Nedko Nedyalkov (c).

feet are whitish. Tail is whitish or more frequently cream or yellowish, monochromatic or slightly darker above (cream-buff) than below (cream-white); densely clad with long stiff hair, concealing the annulation; terminal pencil is 11–13 mm long (Figure 48e). Young are mouse-grey and moult at BWt=20–27 g (Sludskiy et al. 1978).

Skull is extremely flat and further depressed in the interorbital region (Figure 68). Height of the skull behind M^3=4.4–7.2 mm (=16.6–25.7% CbL), height of the braincase with bullae =6.9–9.0 mm, and braincase height without bullae=5.3–7.7 mm (Pozdnyakov et al. 2004). Zygomatic arches are moderately expanded (ZgW/CbL=0.5–0.6); interorbital region is wide (=13.5–18.3% CbL). Supratemporal ridges are

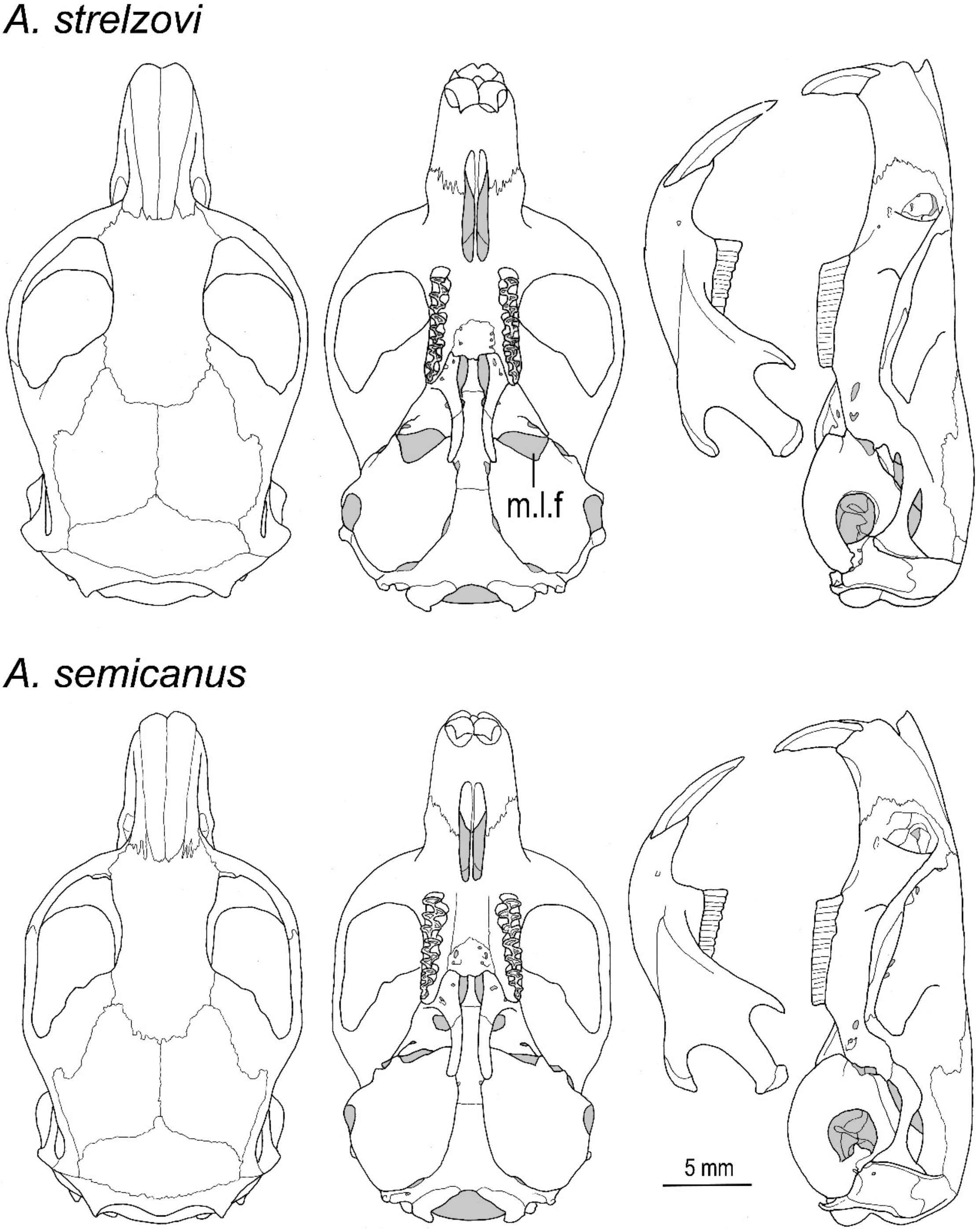


Figure 68: Skull in mountain voles: top–*Alticola strelzovi* (Yustit valley, Kosh-Agach, Altai Republic, Russian Federation); bottom–*A. semicanus* (10 km north-west of Erzin, Erzinskiy Rayon, Tuva, Russian Federation). m.l.f.–middle lacerate fossa.

prominent in adults but remain widely apart; squamosal processes are conspicuous; interparietal bone is large. Incisive foramina are long and usually exceed the level of M^1 alveoli; bullae are rather small and middle lacerate fossae are enlarged (Figure 68). Pterygoid fossae are large but shallow. Mandible is decidedly lower than in other mountain voles; the articular and angular processes are slender and long. Molars are light and weak (Figure 69a–c'); the upper molars are compressed laterally which becomes fully evident in adults. The M^3, which is particularly stretched out, is 1.60–2.15 mm long and 0.60–1.00 mm wide; it is of normal shape with 2 deep re-entrant folds on each side. M$_1$ (length=2.00–2.75 mm; Pozdnyakov et al. 2004) has 3–4 labial re-entrant angles; the alternating triangles T1–T2 and T3–T4 are isolated or confluent; T5 is normally confluent with anterior cap which is either simple oval or with an additional labial triangle (T6); BR4 is rarely deep.

Karyotype (2n=56, NF$_a$=58) consists of 25 pairs of acrocentrics of variable size, 1 pair of large subtelocentric and 1 pair of small metacentric autosomes; X is large acrocentric and Y is small subtelocentric (Orlov & Bulatova 1983, Hielscher et al. 1992, Stubbe et al. 1994).

Variation and subspecies. Ognev (1950) recognised 3 subspecies (*strelzovi, desertorum, depressus*), while Gromov & Polyakov (1977) and Gromov & Erbajeva (1995) accepted 2 subspecies (*strelzovi* with *desertorum* as a synonym, and *depressus*). Phylogenetic analysis of partial sequence for *Cytb* (Chertilina et al. 2012) and a multivariate analysis of skull measurements (Lopatina 2011) retrieved 2 lineages which Lopatina (l.c.) classified as distinct subspecies (*strelzovi* and *desertorum*). They cannot be reliably defined by linear morphometric measurements (cf. data in Pozdnyakov et al. 2004), dental pattern (Pozdnyakov et al. 2017) or colouration.

Molar pattern varies independently of phylogenetic structuring. Morphology of M$_1$ is less variable than that of M^3 and is not associated with environmental factors. On the other hand, structural complexity in M^3 correlates negatively with altitude (Pozdnyakov et al. 2017).

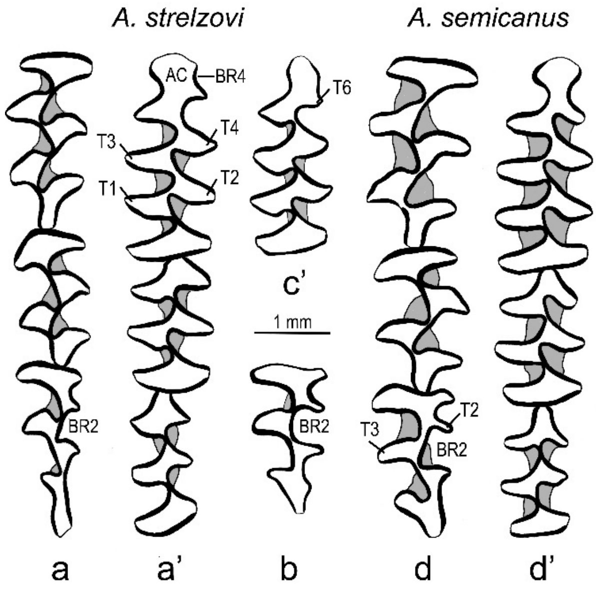


Figure 69: Molar pattern in mountain voles. *Alticola strelzovi*: upper (a) and lower row (a'–20 km west of Kokpekty, Zaysan, Kazakhstan); isolated M^3 (b–E Severo-Chuyskiy Ridge, Altayksiy kraj, Russian Federation) and M^1 (c'–Kara-kuus, 70 km south of Karkaralinsk", Kazakhstan). *A. semicanus*: upper (d) and lower row (d'–Tuva Region, Russian Federation).

Alticola strelzovi strelzovi (Kastschenko, 1899)

Microtus strelzovi Kastschenko, 1899:50 + Figs. 2 & 3 in Table II. Syntypes were from two localities in "Central Altai": "Shores of Lake Ten'ga" and "Bank of River Malaya Ul'gumen"'. Type locality subsequently restricted to the "Shores of Lake Ten'ga" (Ognev 1950:542), now in Altai Republic, Russian Federation.

Synonyms. *M[icrotus] strelzowi* Kastschenko, 1901 [variant spelling of *strelzovi* Kastschenko]; *Platycranius streltzovi* [*sic*] *depressus* Ognev, 1944.

Distribution. Russian Federation (central and south-eastern Altai Mts. in the Altai Republic, and western Tannu-Ola Mts. (Tuva); also Uvs in adjacent north-western Mongolia (Lopatina 2011).

Characteristics. Delimited from *desertorum* by *Cytb* sequence (Chertilina et al. 2012) and in multivariate analysis of skull measurements (Lopatina 2011).

Dimensions: BWt=33–59 g, H&B=109–134 mm, TL=37–53 mm, HF=18.6–22.5 mm, EL=16–21 mm, CbL=26.2–29.7 mm, ZgW=14.5–16.9 mm, MxT=5.5–6.7 mm. Populations are smaller in the Altai Mts. (population means of CbL<26.7 mm) and larger in Tuva (=27.8 mm; Pozdnyakov et al. 2004).

Alticola strelzovi desertorum (Kastschenko, 1901)

M[icrotus] strelzowi desertorum Kastschenko, 1901:206. New name for "*Arv[icola] alliaria* Eversmann" which is preoccupied by Pallas. Eversmann's *alliaria* originated from "the steppes on this side (*sic*) of the Ural Mts. Ridge" (Eversmann 1850:168). Type locality of desertorum subsequently restricted to "Kara-Kuus, 70 km from Karkaralinsk" (Ognev 1944b:185), Karagandy, Kazakhstan.

Synonyms. *A[rvicola] alliaria* Eversmann, 1850 [preoccupied by Pallas].

Distribution. Kazakhstan (including Tarbagatay Mts. and Kalbinskiy Altai) and central Mongolian Altai (Bayan-Ölgiy) (Lopatina 2011). Range includes northern Xinjiang in China (Luo et al. 2000; Wang 2003).

Characteristics. See under nominal subspecies. Dimensions: BWt=32–67 g, H&B=101–133 mm, TL=35–47 mm, HF=19–24 mm, EL=11–20 mm, CbL=24.1–28.8 mm, ZgW=14.1–17.5 mm, MxT=5.2–6.8 mm.

Alticola semicanus (G. M. Allen, 1924) – Khangay (Mongolian) Mountain Vole

Taxonomy. Described as a subspecies of *worthingtoni* (=*argentatus*) and long retained within the scope of *argentatus* (e.g. Ognev 1950, Zhang et al. 1997) or synonymised with *roylei* (Ellerman & Morrison-Scott 1951, Corbet 1978). Status of a species in its own right proposed in Argyropulo (1933) and accepted by Pavlinov & Rossolimo (1987). Phylogenetic reconstructions retrieved close relationships of *semicanus* with *barakshin* and *strelzovi* (Kohli et al. 2014). Under experimental conditions, *semicanus* did not hybridise with *barakshin, argentatus* or *severtzowi* (Stubbe et al. 1994).

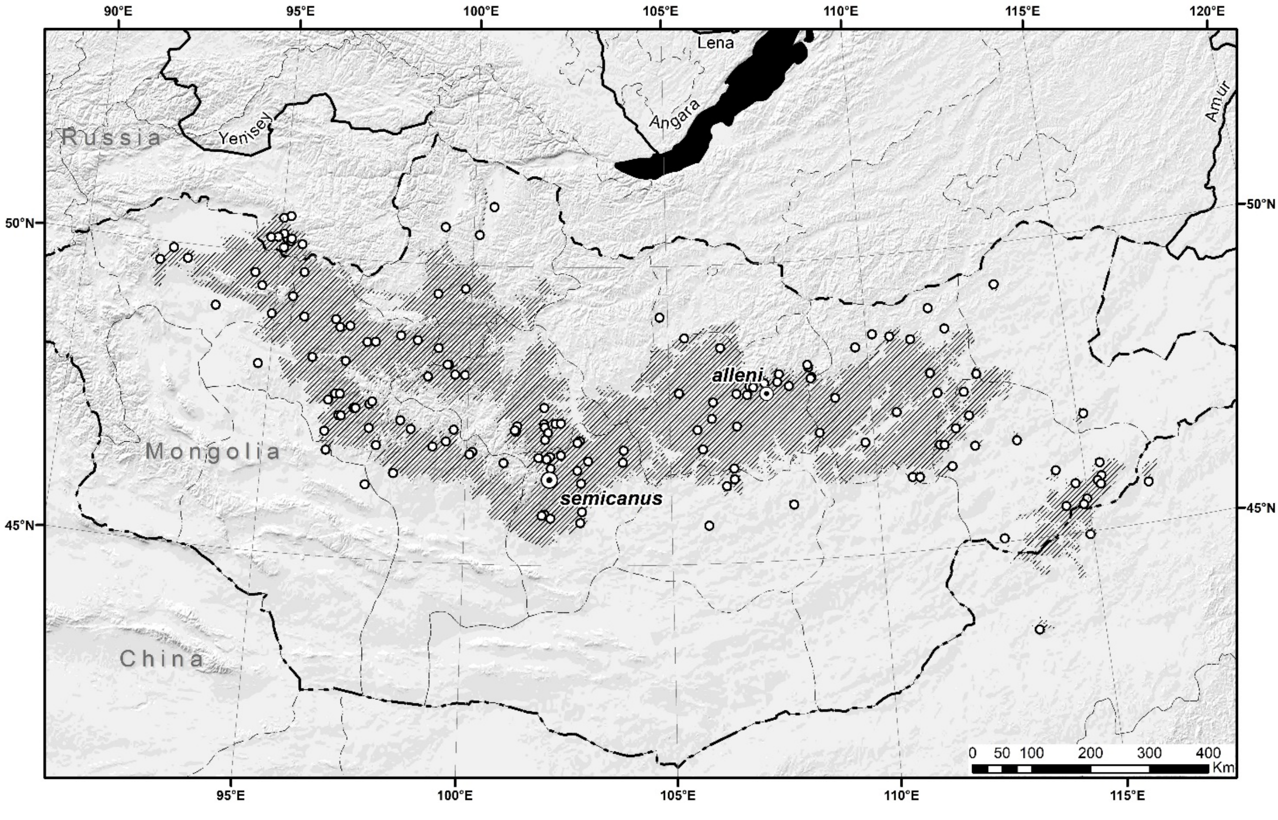


Figure 70: Distributional range of the Khangay mountain vole *Alticola semicanus*.

Distribution (Figure 70). The vast majority of the range is in northern, central, and eastern Mongolia, specifically on the Han-Huhiyn Ridge, Khangay, Hentii, and the low mountains of south-eastern Mongolia. The range also encompasses the southern Tuva Region (Russian Federation), and reaches Xilingol League (Inner Mongolia, China) in the south-east. The area is estimated to cover 336,500 km^2. Habitat is dry undulating landscape at 900–3,900 m a.s.l. with a shallow soil layer, plenty of gravel and sparse vegetation (<30% surface cover) of xerophytes. Voles live among rocks, boulders and on rocky outcrops with a supply of grass (Allen 1940, Xu 2016). The shape of the fragments follows the topography of the mountainous terrain (Luo et al. 2000).

Characteristics. A large and short-tailed (TL/H&B=0.18–0.32) mountain vole with large ears and long whiskers (Figure 67c). Dorsal pelage is grey, occasionally shaded buff and slightly darkened by scattered black tips; upper lips, cheeks and hair around the ears are pinkish buff. Underside and flanks are buffy white and demarcation against the grey back is sharp; some animals may have an indistinct pinkish-buff lateral line. Ears are grey, paws whitish grey; tail is nearly white, densely clad with stiff hairs; terminal pencil is long (7–12.5 mm) (Figure 48f). Skull is large, elongated and moderately deep (height behind M^3=27.5–31.5% CbL) without prominent ridges or crests; squamosal processes are minute (Figure 68). Zygomatic arches are moderately bowed (ZgW/CbL=0.55–0.6), interorbital region is flat and wide, incisive foramina short; interparietal large. Dorsal profile of the skull is slightly depressed over the orbital region. Dental pattern varies only slightly (Rossolimo & Pavlinov 1992). M^3 is 6–21% longer than M^2 with 2 deep re-entrant angles on each side. The antero-labial triangle T2 is rudimentary and, together with AL, isolated from the dental field of T3; the dental fields of T3, T4 and a short posterior cap are normally confluent and less commonly isolated (Figure 69d). In some individuals an additional lingual salient angle may be present on M^3 (Bannikov 1954).

Karyotype (2n=56, NF$_a$=60) contains 1 large subtelocentric and 1 small metacentric pair while the remaining autosomes are acrocentric. The X is large acrocentric and Y is small subtelocentric or submetacentric (Hielscher et al. 1992, Stubbe et al. 1994). In the results from Orlov et al. (1978), autosomes are acrocentric, except for the small metacentric pair; heterosomes are also acrocentric.

Variation and subspecies. Rossolimo & Pavlinov (1992) distinguished 2 subspecies but noted that "variation … is rather continuous". Under captive conditions, these subspecies produced fertile hybrids (Stubbe et al. 1994). Although the subspecies are loosely defined and intergrade in eastern Khangai Mts. (Rossolimo & Pavlinov 1992), we list them as distinct taxa.

Alticola semicanus semicanus (G. M. Allen, 1924)

Microtus (Alticola) worthingtoni semicanus G. M. Allen, 1924:6. Type locality: "Sain Noin Khan, Mongolia".

Distribution. Western and central Tuva and the Khangai Mts.

Characteristics. Dorsal pelage more brownish, frequently with a distinct buffy stripe along the flanks. Dimensions: BWt=24.5–64 g, H&B=101–135 mm, TL=20–34 mm, HF=17–22 mm, EL=14–20 mm, CbL=25.1–31.4 mm, ZgW=13.9–17.9 mm, MxT=5.6–7 mm.

Alticola semicanus alleni Argyropulo, 1933

Alticola (Alticola) semicanus alleni Argyropulo, 1933:180. Type locality: "Kentej [Kentai] Mountain range, 40 km east of Urga (Ulan-Bator-Choto), ca. 1000 m a. s. l., North Mongolia". Not part of *A. macrotis* (Allen 1940:841) but a of *semicanus* (our examination of the type series).

Distribution. Eastern Mongolia (Rossolimo & Pavlinov 1992) and Inner Mongolia (Luo et al. 2000; Xu 2016).

Characteristics. Dorsal pelage more greyish, flanks lack buffy stripe. Dimensions: BWt=28–65 g, H&B=93–130 mm, TL=25–37 mm, HF=13–23 mm, EL=13–20.5 mm, CbL=26.1–29.6 mm, ZgW=14.6–17.1 mm, MxT=6–6.9 mm.

Alticola tuvinicus Ognev, 1950 – Tuva Mountain Vole

Taxonomy. Described as a species in its own right but frequently synonymised with *A. argentatus* or *A. roylei.* Species rank re-established in Pavlinov & Rossolimo (1987). In the past *tuvinicus* also included *olchonensis* (see under that species). Most closely related to *olchonensis* and *semicanus* (Litvinov et al. 2015, Bodrov et al. 2016)

Distribution (Figure 71). Distributional range (=109,430 km²) is in 3 isolates in the Russian Federation and Mongolia: (i) Kuznetsk Alatau Mts., (ii) Tuva (Yenisey Valley and the ridge of eastern Tannu-Ola) and Mongol Altai, and (iii) northern shores of Lake Khubsugul (south-eastern edge of Eastern Sayan Mts.). Altitude in Khakasia and Tuva is 450–2,990 m while in Mongolia *tuvinicus* was recorded >1,800 m a.s.l. The vole occupies rocky slopes with shrubs and was recorded inside caves (Litvinov et al. 2014); it is not abundant anywhere and a decline has been reported in Khakassia "in recent decades" (Abramov et al. 2019).

Characteristics. Size moderately large; ears are large and semi-circular (Figure 67e), whiskers are long (43–46 mm); tail is densely clad with stiff hair which terminates in a long pencil (length=8–15 mm; Figure 48h). Fur is soft, ash grey above with wood brown stain; cheeks and underside are greyish; delimitation between a brownish grey back and a greyish belly is distinct. Ears are plain grey; feet are whitish and tail is light. Skull is lightly built and shallow (Figure 72); height behind M^3=25.7–31%

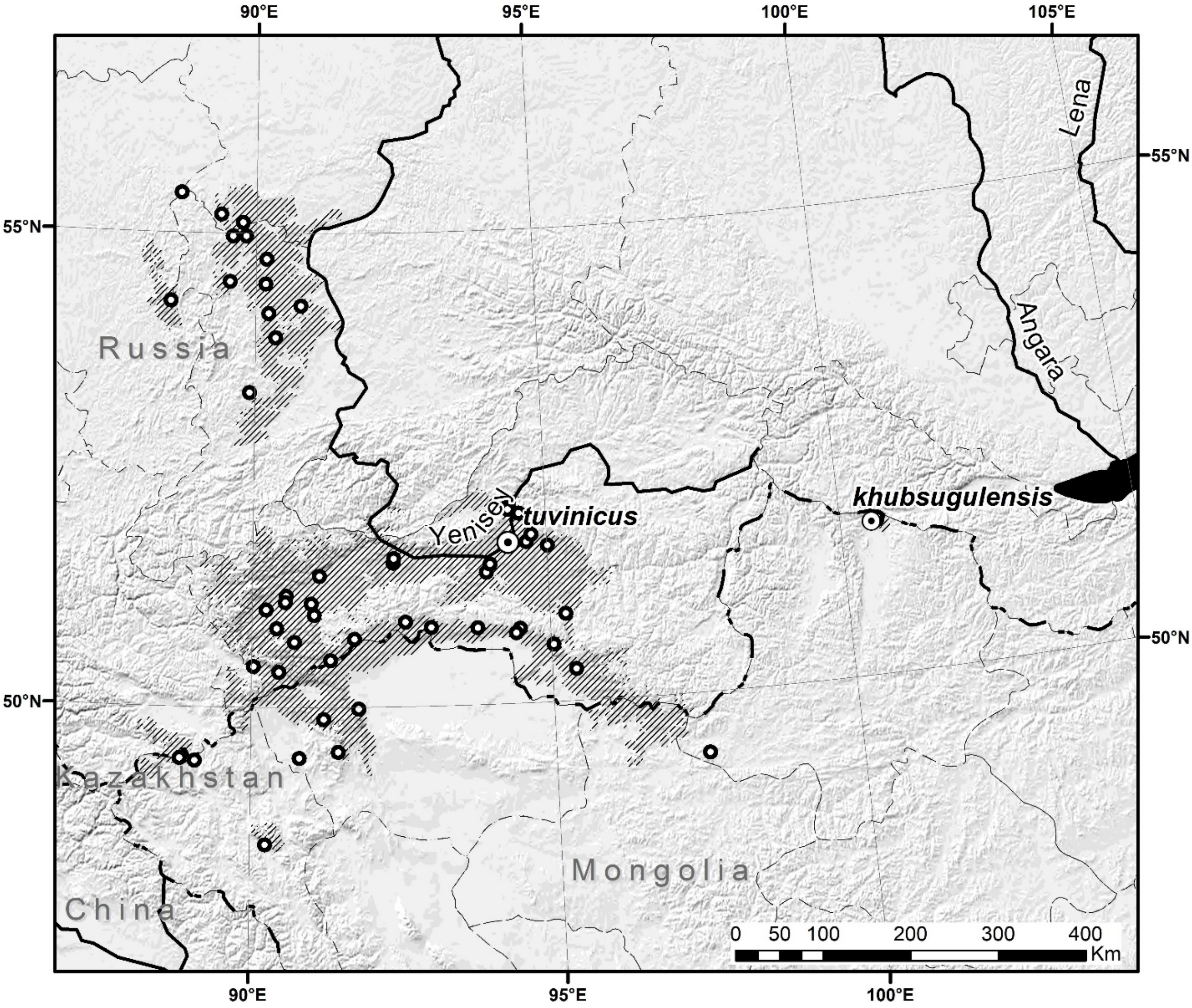


Figure 71: Distributional range of the Tuva mountain vole *Alticola tuvinicus*.

CbL. Zygomatic arches are rather narrow (ZgW/CbL=0.54–0.58); braincase is narrow. Interorbital region is wide; rostrum long and narrow, orbit long and with a weak squamosal process. Incisive foramina do not reach the level of M^1. M^3 is longer than M^2 by 14–30%, normally with 2 re-entrant angles on each side (Figure 73a-c).

Variation and subspecies. Rossolimo & Pavlinov (1992) recognised 2 subspecies.

Alticola tuvinicus tuvinicus Ognev, 1950

Alticola tuvinicus Ognev, 1950:520. Type locality: "Tuvinskaya Autonomous oblast [Tuvan Republic], vicinity of town Kyzyl", Russian Federation.

Distribution. The entire range of the species except the isolate in the south-western edge of Eastern Sayan Ridge (Bolshoy Sayan).

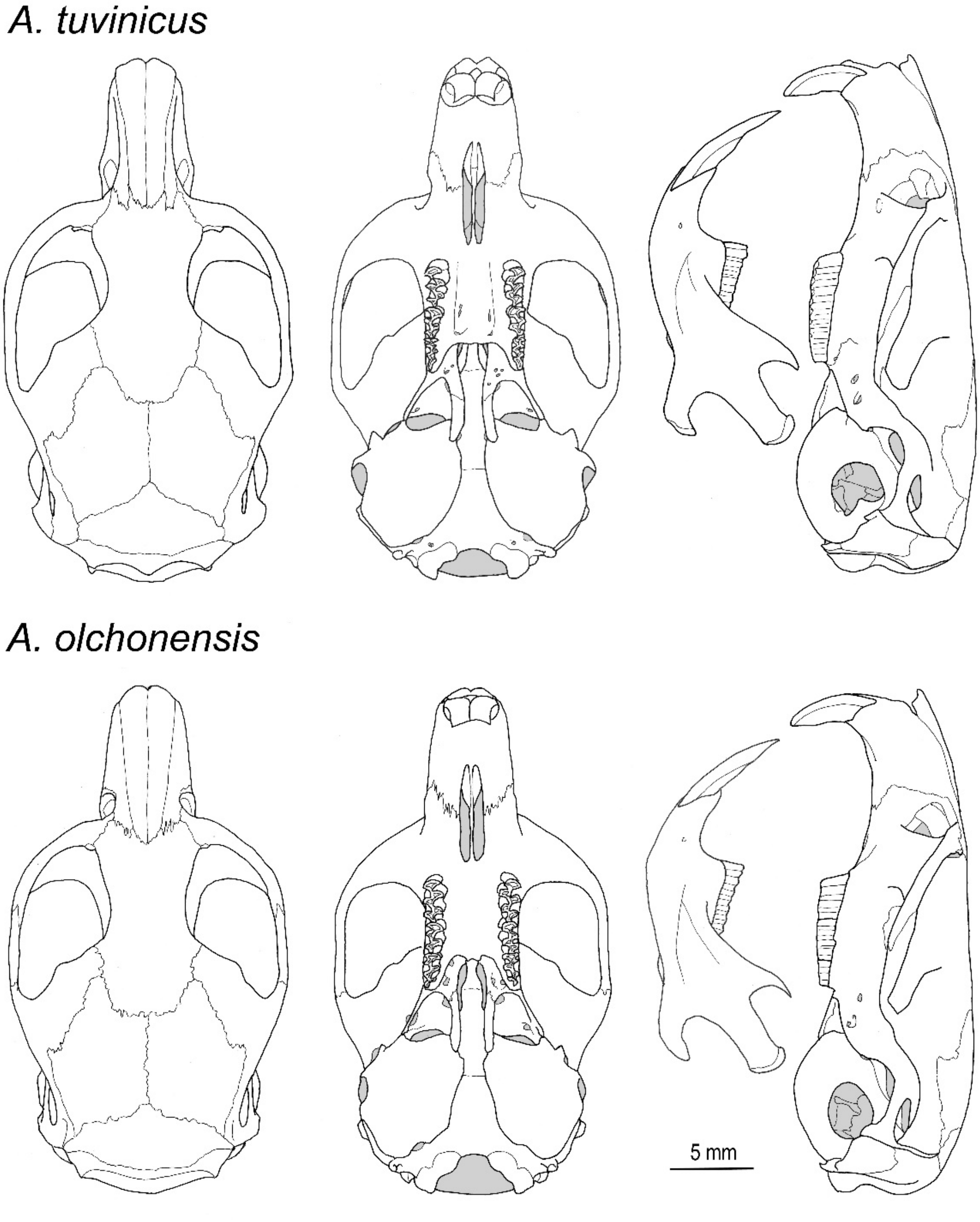


Figure 72: Skull in mountain voles: top–*Alticola tuvinicus* (22 km east of Uyuk, Piy-Khemskiy Rayon, Tuva Region, Russian Federation); bottom–*A. olchonensis* (Lake Baikal, Russian Federation).

Characteristics. Back more brownish; tail shorter (TL/H&B=0.32–0.46; Figure 48h), indistinctly bi-coloured (greyish above, cream below), terminal pencil shorter (6–10.5 mm). Dimensions: BWt=27.5–54.5 g, H&B=99–125 mm, TL=36–49 mm, HF=18–22 mm, EL=12.5–20 mm, CbL=24.1–29.1 mm, ZgW=14.3–16.9 mm, MxT=5.5–6.9 mm.

Alticola tuvinicus khubsugulensis Litvinov, 1973

Alticola khubsugulensis Litvinov, 1973:206. Type locality: "northern shore of Lake Khubsugul in MPR [Mongolian People's Republic]" (p. 208).

Synonyms. *Alticola kosogol* Litvinov, 1973 [nomen nudum].

Taxonomy and nomenclature. Russian authors (Rossolimo et al. 1994, Abramov et al. 2019) use *kosogol* as the senior synonym. Litvinov (1973) quite surprisingly introduced 2 names for the same geographic sample: "*Alticola khubsugulensis* subspecies (*sic*) nova" (p. 206) and "*A. kosogol* sp. nov." (p. 209). The name *kosogol* is mentioned in the Abstract (and only there), which is written in Mongolian (Litvinov 1973:208) and English (p. 209). There is no description and designation of the type, hence *kosogol* is indisputably a nomen nudum. On the other hand, *khubsugulensis* fulfils the requirements of the Code and is an available name. Borissenko et al. (2001:199) interpreted these names as objective synonyms, and Rossolimo et al. (1988:436) claim they are alternative names although Litvinov (1973) did not use such a term. Rossolimo et al. (l.c.) used the Principle of the First Reviser to determine the precedence of *kosogol* over *khubsugulensis*. This is invalid as it supressed the available name (*khubsugulensis)* and gave priority to the unavailable name (*kosogol*).

Distribution. Known only from the northern shores of Lake Khubsugul at 1,645 m a.s.l. This is a geographic isolate situated >300 km eastward of the main range. Voles occupy rocky outcrops in sparse woodlands of aspen and larch (Litvinov & Bazardorzh 1992).

Characteristics. Back more greyish; tail longer (TL/H&B=0.46–0.5; Figure 48i), sharply bi-coloured (blackish-brown above, white below), terminal pencil longer (=9.5–15.5 mm). Dimensions: H&B=100–120

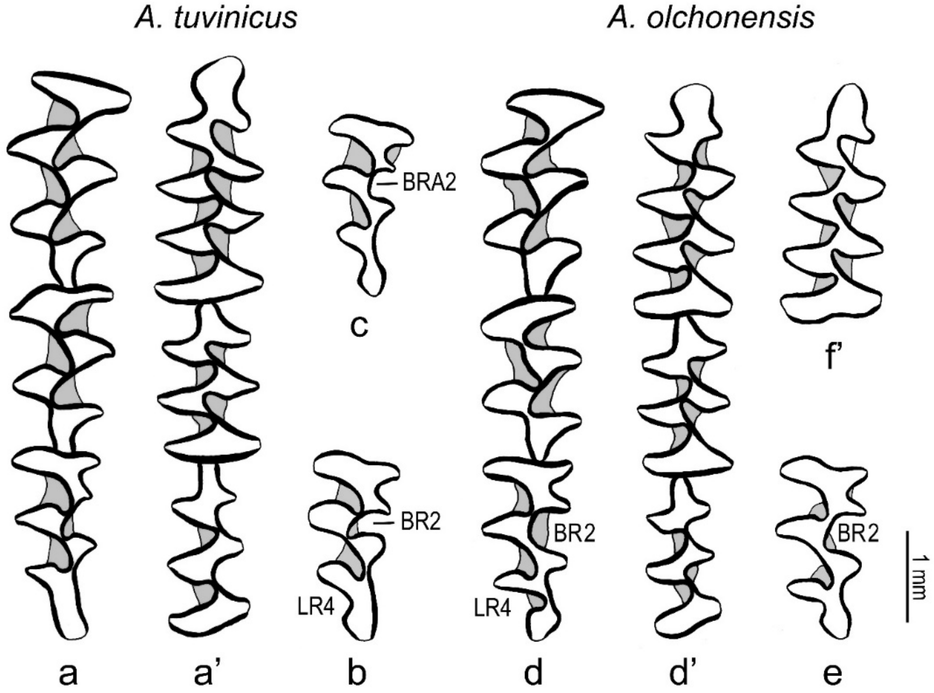


Figure 73: Molar pattern in mountain voles (all from Russian Federation). ***Alticola tuvinicus*****: upper (a) and lower row (a'–Tuva); isolated M^3 (b & c–both from 22 km E of Uyuk, Piy-Khemskiy Rayon, Tuva Region).** ***A. olchonensis*** **(all from Lake Baikal, Irkutsk Oblast): upper (d) and lower row (d'); isolated M^3 (e) and M$_3$ (f'). Specimens (d) & (f) are from O'lkhon Is.**

mm, TL=56–60 mm, CbL=25.7–28.2 mm, ZgW=13.8–15.7 mm, MxT=5.8–6.5 mm.

Alticola olchonensis Litvinov, 1960 – Baikal Mountain Vole

Alticola argentatus olchonensis Litvinov, 1960:1889. Type locality: “Olkhon Island on [Lake] Baikal”, Russian Federation.

Synonyms. *Alticola baicalensis* Litvinov, 1961.

Taxonomy. Described as a subspecies of *argentatus*; some authors synonymised *A. olchonensis* with *roylei* (Corbet 1978) or *A. tuvinicus* (Rossolimo et al. 1988). Gromov & Polyakov (1977) synonymised *olchonensis* with *macrotis*, which caused some authors to classify it in *Aschizomys* (e.g. Musser & Carleton 2005). Analysis of nuclear and *Mt*-genes (Litvinov et al. 2015, Bodrov et al. 2016), and of molar (M^3) morphology (Vasil’eva et al. 2016) showed that *olchonensis* is a species in its own right, a member of *Alticola* s. str., and possibly a sister species to *tuvinicus*.

Distribution (Figure 74). Known from a small area (=334 km^2) between the lower Anga River and the Olkhonskiye Vorota strait on the north-eastern shore of Lake Baikal, and the Baikal islands in the Maloye More Strait (Borakchin, Kharantsy, Khibyn, Malyy Toynik, Ogoy, Zamogoy), and O’lkhon Island. The range encompasses undulating landscape with abundant rocky places and is characterised by a dry climate (Litvinov 2007). Specimens were collected at altitudes of 450–680 m a.s.l.

Characteristics (Figure 67f)**.** Dimensions: BWt=24–47 g, H&B=102–124 mm, TL=31–43 mm, HF=18–22 mm, EL=14–19 mm, CbL=26.1–28.9 mm, ZgW=14.4–16.1 mm, MxT=6.2–6.9 mm; tail is rather short (TL/H&B=0.27–0.37; Figure 48j). Fur is soft and long (up to 13.5 mm), the back is grey with a rusty tint and buff behind the ears. The belly is white to silvery-grey; it is clearly demarcated from the back. Grey ears are margined buff; the snout is also buff. Tail is distinctly bi-coloured, white below and greyish above, frequently with additional a darker narrow medial stripe; the terminal pencil is long (8–15 mm). Feet are grey. Skull is lightly built, moderately deep (height behind M^3=27.5% CbL; height across bullae=36% CbL) and with weakly bowed zygomatic arches (ZgW/CbL=0.53–0.58). Incisive foramina are short, terminating in front of the anterior edge of M^1 (Figure 72). The enamel pattern of M^3 is distinct: BR2 is of a square shape (rarely seen in other species of *Alticola*) and the posterior loop is frequently constricted by a deep LR4 (Figure 73d-f).

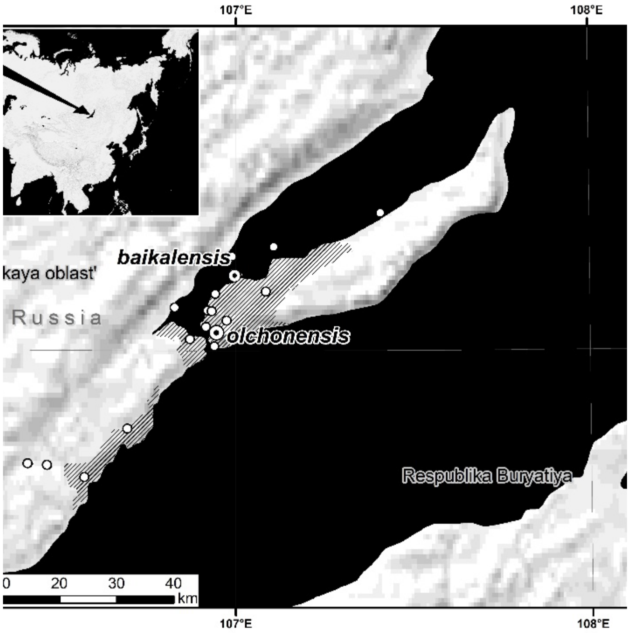


Figure 74: Distributional range of the Baikal mountain vole *Alticola olchonensis*.

Variation and subspecies. Monotypic species. Variation in skull morphology and molar pattern was reported among the island populations. Voles from O’lkhon are the largest and those from Borokchin are the most distinct in shape. Shape dissimilarity is not associated with geographic distances between the islands (Abramov et al. 2017).

SUBGENUS: *Aschizomys* Miller, 1899

Aschizomys Miller, 1899b:369. Type species: *Aschizomys lemminus* Miller.

Nomenclature. The year of publication of *Aschizomys* is sometimes reported as 1898 (e.g. McKenna & Bell 1997:154). The print copy of the Proceedings for 1899, pages 257–320, with Miller’s naming of *Aschizomys*, were mailed to the Academy of Natural Sciences of

Philadelphia on July 26, 1899, and presented on August 1 of the same year.

Taxonomy. The subgenus contains 2 species that are clearly distinct morphologically and genetically. *A. macrotis* captured *Mt*-DNA of *lemminus* during a secondary contact at ~22 kya; nuclear genes, however, retrieved reciprocal monophylly between the two species (Bodrov et al. 2020).

Distribution. Northern part of the range of *Alticola*. Ranges of the two subgenera overlap in the Altai, wider area of Lake Baikal, and northern Mongolia.

Characteristics. The tail is short, thick, and densely clad by hair that conceals the underlying annulation (Figure 48k,l). The skull shows no peculiarities and resembles that found in *Clethrionomys*; in comparison to subgenus *Alticola*, the incisive foramina are markedly short. Molar pattern closely resembles *Clethrionomys* or *Craseomys*; re-entrant angles are abundantly filled with cementum and salient angles are rounded. Enamel is undifferentiated and the schmelzmuster contains at least some lamellar enamel; the convex (leading) edges of triangles also usually comprise the tangential type (Koenigswald 1980).

Alticola macrotis (Radde, 1861) – Large-eared Vole

Taxonomy. Two junior synonyms of macrotis were treated as independent species in the past: *altaica* (Vinogradov & Argyropulo 1941) and *vinogradovi* (Ognev 1950); hybrids between *macrotis* s.str. and *vinogradovi* are fertile (Kuznetsova 1992). We adopted the taxonomic scope of *macrotis* as defined in Vasilyeva et al. (2008).

In the past *macrotis* captured some *Mt*-DNA from *C. centralis* (Kohli et al. 2014); the current ranges of these two voles do not overlap. The alien sequences incorrectly aligned *macrotis* with *Clethrionomys* (Cook et al. 2004, Tang et al. 2018).

Distribution (Figure 75). Mountains of Central Asia in eastern Kazakhstan, southern Siberia (Russia), Mongolia and northern Xinjang (China): Altai, Kuznetskiy Alatau, Sayan, Khamar Daban, Hangay, Tannu-Ola, and the mountain ridges of south-eastern Transbaikal (Sokhondo, Daursky, Tschreskogo and Yablonovy). The range covers an estimated 112,700 km². Principal habitats are accumulations of rocks and boulders in the high mountain steppe, sub-alpine zone, alpine meadows and lichen tundra. Altitudinal range is 750–3,580 m a.s.l.

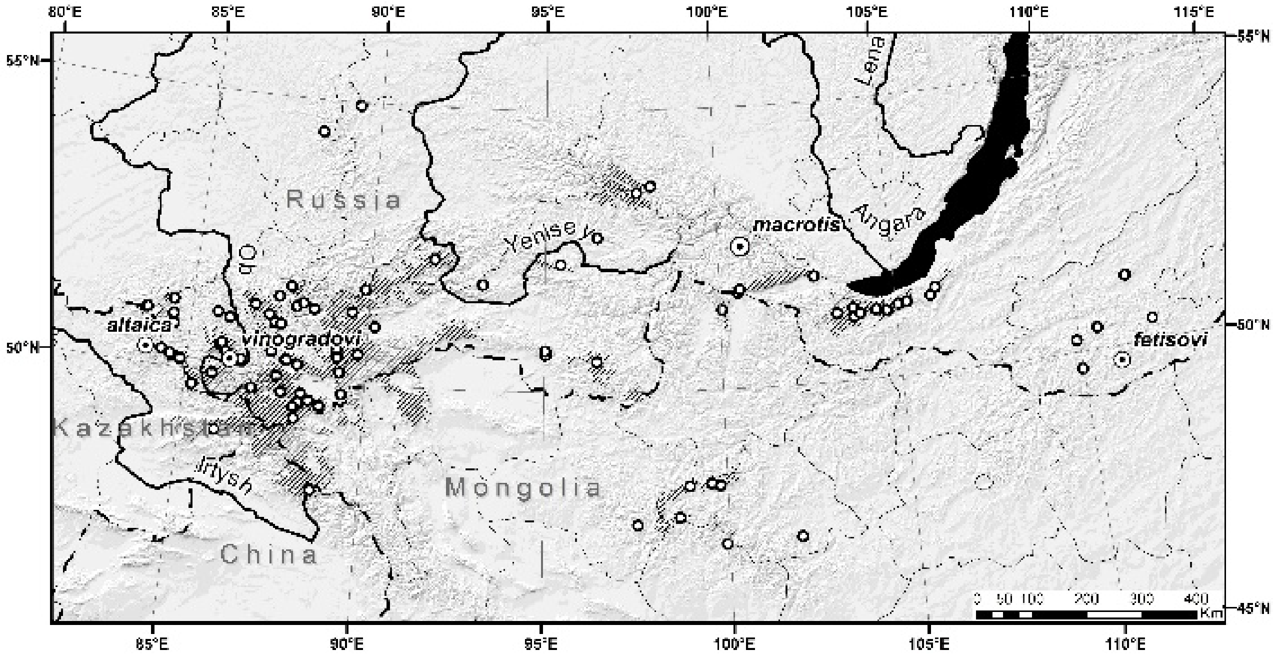


Figure 75: Distributional range of the Large-eared vole *Alticola macrotis*.

Figure 76: Carcass of *Alticola macrotis* collected at Peak 9th Stanciya, above Aktash, Altai Republic, Russian Federation. Photo: B. Kryštufek.

Characteristics. A moderately large and corpulent vole (Figure 76). Tail is rather short (TL/H&B=0.17–0.34); relative length varies among populations and is densely clad with hair and terminates in a prominent, long (12 mm) pencil (Figure 48k). Ears are large and semi-circular. Fur is soft and moderately long. Palmar and plantar surfaces are hairy to the pads; relative to interdigital pads, the metacarpal pads are larger and the metatarsal pads are smaller (Figure 77). Hair is grey with brown (drab to cinnamon-buff) hues on the back. Flanks and belly are grey, frequently tinted buff; hair bases are slate and those on the belly have white tips. The tail is sharply bi-coloured in ~70% of voles (Sludskiy et al. 1978), dark greyish brown above, white or silver below. Paws are light grey. Females have 8 nipples. The skull has moderately expanded zygomatic arches (ZgW/CbL=0.52–0.57); braincase and incisive foramina are short; bullae are of modest size (Figure 78). The M^3 is of a simple structure with 2 inner re-entrant angles; the 3rd re-entrant angle is rarely present in adults (Figure 79a,b) but can be seen in young animals (Galkina & Yepifantseva 1988). The antero-labial triangle T2 is of normal size and is largely isolated from the alternating T3 on the lingual side. The length of M^2 is highly variable depending on the subspecies. M_1 is with 3–4 lingual and 3 labial re-entrant angles. Triangle T5 opens into anterior cap; its connection with the alternating T6 is frequently wide.

Karyotype (2n=56) includes 25 acrocentric pairs and a pair of small metacentrics. The X is large acrocentric; Y is small and consists entirely of C-heterochromatin (Bolshakov et al. 1985).

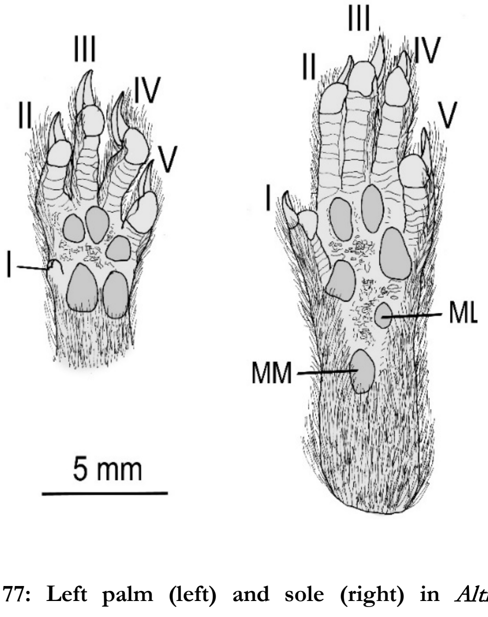


Figure 77: Left palm (left) and sole (right) in *Alticola macrotis* (Chikhacheva Ridge, Altai, Russian Federation).

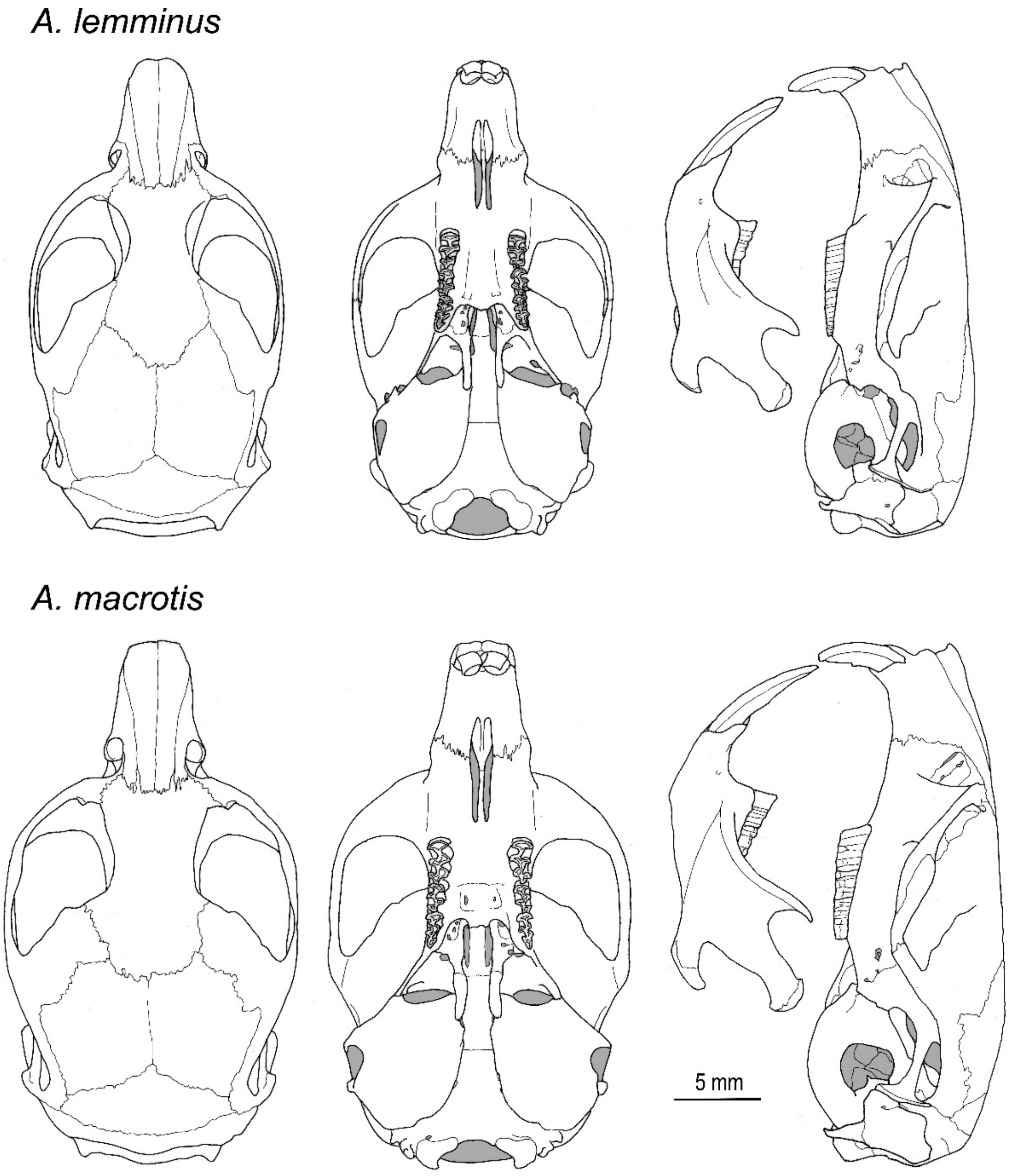


Figure 78: Skull and mandible in *Alticola* (*Aschizomys*) mountain voles (both from Russian Federation): top–*A. lemminus* (Lake Grand, Atka, Magadan); bottom–*A. macrotis* (valley of R. Yustyd near Kosh-Agach, Altai Republic).

Variation and subspecies. Interpopulation phenotypic variation in nonmetric cranial traits (Vasil'eva 1999), molar pattern (Bolshakov et al. 2012) and other morphological traits (Vasilyeva et al. 2008) was addressed in wild and captive populations. Two groups emerged in the majority of studies and were classified as distinct subspecies. Bolshakov et al. (2012) suggested the rank of independent species for *fetisovi*. Recent phylogeographic analysis retrieved 3 *Mt*-lineages; the most divergent group corresponds with *fetisovi* (Bodrov et al. 2020).

Alticola macrotis macrotis (Radde, 1861)

Arvicola macrotis Radde, 1861:681. Type locality: "altitudes above 7000' [2,130 m] in Eastern Sayan Mts.", Siberia, Russian Federation.

Synonyms. *Alticola altaica* Vinogradov, 1933; *Alticola vinogradovi* Razorenova, 1933.

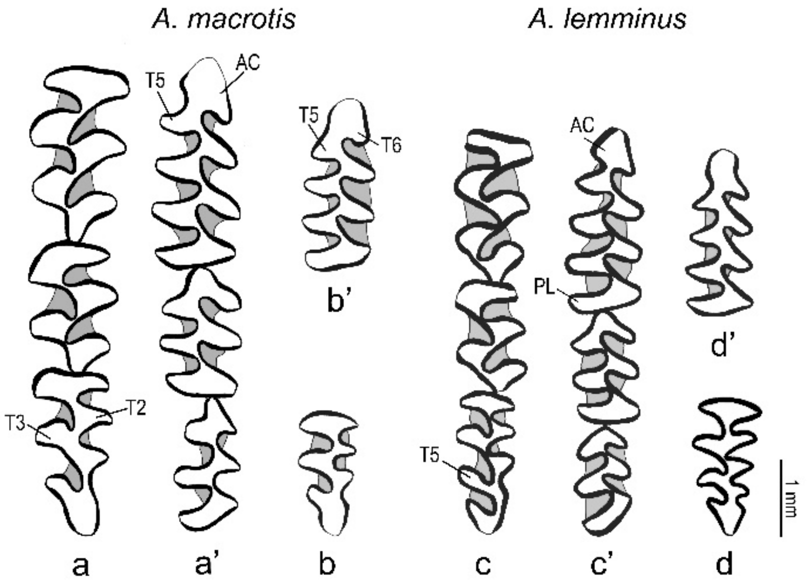


Figure 79: Molar pattern in *Alticola* (*Aschizomys*) voles (all from Russian Federation). *Alticola macrotis*: upper (a) and lower molar rows (a'–Terektinskiy Ridge, Central Altai Mts.); isolated M^3 (b) and M_1 (b'–Sokhondo, North Khentei, Transbaikalia). *A. lemminus*: upper (c) and lower molar rows (c'–Butugychag, Kolymsk Range); isolated M^3 (d) and M_1 (d'–Butugychag, Kolymsk Range).

Distribution. The majority of the species' range from Sayan and Altai to the Baikal region (Vasilyeva et al. 2008).

Characteristics. M^3 is long (1.86–2.08 mm) and simple (3 lingual salient angles). Populations from the trans-Baikal region tend to have a more complex pattern than those from the Altai. Dimensions: BWt=21–47.5 g, H&B=93–123 mm, TL=18–46 mm, HF=17–21 mm, EL=12–17 mm, CbL=24.1–26.8 mm, ZgW=13.2–15.3 mm, MxT=5.3–6.7 mm. Size varies among populations; skull is longest in the Baikal region ($\bar{x}$ CbL=26.39 mm) and shortest in Tuva ($\bar{x}$ CbL=25.5 mm; Vasilyeva et al. 2008).

Alticola macrotis fetisovi (Galkina & Jepifantseva, 1988)

Alticola fetisovi Galkina & Epifantseva, 1986:128. Type locality "Sokhondo", 2,100–2,300 m a.s.l., North Khentei, Transbaikalia (Galkina & Yepifantseva 1988), Russia.

Distribution. High altitudes (2,100–2,300 m) in Sokhondo, south-western spur of Daurian Ridge and likely also Tschreskogo and Yablonovy Ridges in south-eastern Trabnsbaikal area (Russian Federation).

Characteristics. Size small: H&B=104–113 mm, TL=18–24 mm, HF=15.2–17 mm, EL=13.4–14.5 mm, CbL=25–26.1 mm, ZgW=13.8–14.3 mm, MxT=5.2–5.4 mm. Tail is short; M^3 is distinctly short (1.55–1.70 mm; Galkina & Yepifantseva 1988).

Alticola lemminus (Miller, 1899) – Lemming Vole

Aschizomys lemminus Miller, 1899b:369. Type locality: "Kelsey Station, Plover Bay [zaliv Kresta], Bering Strait". Chukotka Autonomous Okrug, Russian Federation.

Synonyms. *Alticola macrotis vicina* Portenko, 1963; *A[schizomys] l[emminus] jacutensis* Vasil'eva & Vasil'ev, 1992 [nomen nudum]; *A[schizomys] l[emminus] yakutensis* Vasil'eva, 1999 [nomen nudum].

Taxonomy. The lemming vole was classified in *Clethrionomys* or *Eothenomys* in the past but was frequently synonymised with *A. macrotis* (see accounts on *Alticola* and *Aschizomys*).

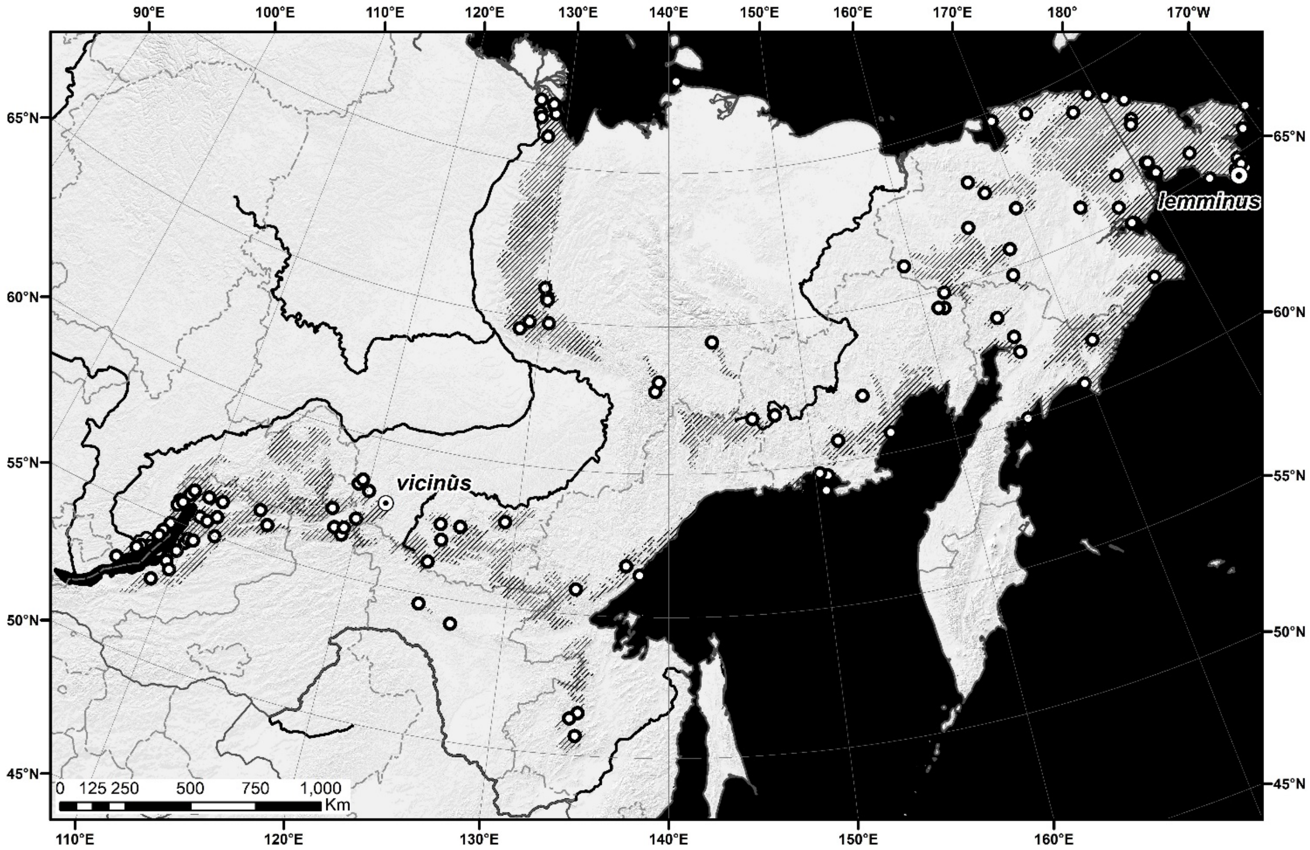


Figure 80: Distributional range of the lemming vole *Alticola lemminus*.

Distribution (Figure 80). Tundra and taiga in north-eastern Siberia and northern Far East, between the Lena and Chukotka Rivers, and from the shores of the Arctic Sea to the coasts of the Sea of Okhotsk and the Bering Sea. The southernmost records are in mountain ridges bordering Baikal Lake from the north (Baykalskiy, Barguzinskiy, Golondinskiy and Ikatskiy), and the Badzhal'skiy and Bureinskiy ridges. Distributional range covers 917,500 km^2 but is highly fragmented; *lemminus* is not present in Kamchatka. With the exception of isolated records in the estuary of the Lena River, the south-western margin of Verkhoyansk Mts., Kharaulakhskij Mts., and Svyatovy Nos-Mys (Tavrovskiy et al. 1971), *lemminus* is seemingly absent from the majority of eastern Siberia. It occurs on the islands of Olskiy (Zavyalova) in the Sea of Okhotsk, and on Yttygran (Bering Sea).

The lemming vole is common to abundant, albeit sporadic, on mountain slopes and in river valleys. Habitat consists of rocky patches (screes) with dense cover of lichens and mosses; accumulations of large boulders or of small stones are avoided. Vertical range 0–2,377 m.

Description. A small vole with a short tail (TL/H&B=0.16–0.20), blunt muzzle and broad rounded ears that overtop the fur. Dimensions: BWt=23–39 g, H&B=90–115 mm, TL=12–22 mm, HF=15–18.1 mm, EL=12–15 mm, CbL=24–26.5 mm, ZgW=13.2–15.2 mm, MxT=5.2–7 mm. Distal half of the tail is covered with long bristles terminating in a long (6–9 mm) pencil (Figure 48l). Eyes are moderately large and mystacial vibrissae are long. Feet are broad, thumb is vestigial with a flattened nail; claws are moderately developed and overhung by long hairs. Palms and soles have 5 and 6 pads, respectively. The sole is hairy from the heel to the posterior pad. Fur is long, dense and soft; hair in summer (mid-dorsal/mid-ventral length=10–11/4.8–6 mm) is shorter than in winter (12.5–17/6–8.5 mm). Summer fur varies from mouse-grey with various admixture of buff to clear brown; flanks are lighter and more greyish; belly is whitish to light silver-grey, occasionally faintly washed buffy and irregularly darkened by the slate hair bases; demarcation on the flanks is rather sharp. Behind each ear is an indistinct light subauricual tuft. Feet are the same colour as the belly and the tail is sharply bi-coloured, blackish-brown above and whitish below. Young are a similar colour to adults or slightly more grey (Ognev 1950). At least some northern populations (northern Chukotka, Verkhoyansk and Kharaulakhsk Mts.) acquire white winter pelage (Figure 81) with cream or greyish shades on the back; hair bases remain slate. Snout is buff and the eye-ring is conspicuously brownish. Approximately 6% of voles from the Kolyma Mts. and certain southern populations (e.g. from southern Sakha and the Koryak Mts.) retain summer colour during winter (Kistschinsky 1966). Pelage moults in April–early July and again in early September–late October (Revin 1989). Females have 8 nipples.

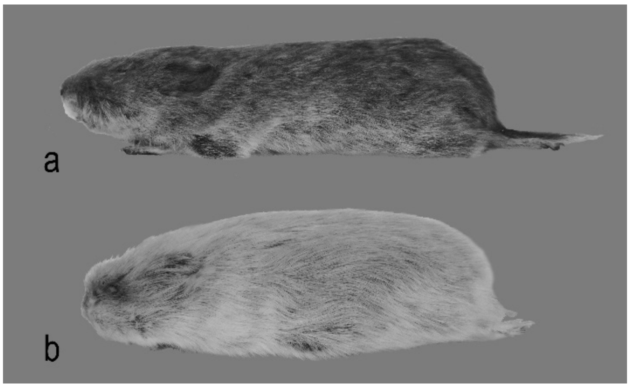


Figure 81: Skins of *Alticola lemminus* from Olekminskiy rayon, Sakha, Russian Federation in summer (a) and white winter pelage (b). Individuals were collected on July 20 (a) and December 5 (b), respectively. Photo: B. Kryštufek.

Skull closely resembles *A. macrotis* (Figure 78), however the braincase is longer and the zygomatic arches are slightly more bowed (ZgW/CbL=0.55–0.58). M^2 forms a conspicuous bulge at the mouth of the sphenoorbital fissure. M_3 is displaced lingually by the shaft of the incisor and encapsulated. M^3 is complex with 3 deep lingual and 2–4 labial re-entrant angles (Figure 79c-d); M_1 has 5 alternating dentine triangles. The triangles may either be closed (Figure 79c') or partly confluent (Figure 79d') depending on age and population; dental fields tend to be more isolated than in *macrotis*. Re-entrant angles are filled with cement.

Diploid number of chromosomes is stable (2n=56) but the morphology of 3 autosomal pairs (Nos. 1, 5, 9) and of both heterosomes differ between populations (Bykova et al. 1978).

Variation and subspecies. Chromosomal caused some authors (Bykova et al. 1978; Vasilyeva et al. 2008) to suggest recognition of lemming voles from Chukotka and from N Sakha as a distinct species.

Phylogeographic assessment uncovered deep genealogical structuring with strong geographic associations. Of the 4 allopatric lineages, the one occupying the triangle between Lake Baikal–Dzugdzhur Mts. (Khabarovsk Krai)–Khayata Range (Yakutia) is the most ancient, followed by an isolate in Burenskiy Range (Khabarovsk Krai). The remaining lineages occupy the Verkhoyansk Range, and the north-eastern part of the distribution to the east of the upper reaches of Kolyma (Bodrov et al. 2020). The name *vicina* is available for the most distinct lineage. Multivariate analyses of morphological traits retrieved 2 main groups of populations: (i) from the middle and lower reaches of the Lena River, and (ii) the upper reaches of the Lena, the Kolyma Mts., and Chukotka. The latter group has a smaller skull and tends towards closed dental fields on M^3 (Vasil'eva 1999; Vasilyeva et al. 2008). The two groups seemingly concur with chromosomal differentiation (Bykova et al. 1978; Bolshakov et al. 1985).

GENUS: *Craseomys* Miller, 1900 – Grey-sided Voles

Taxonomy. We classify 5 species of *Craseomys* into 2 subgenera. The predominantly rhizodont *Craseomys* contains *rufocanus* and *rex*, while the remaining species are in the arhizodont *Phaulomys*. In the past, rhizodont forms were classified as *Clethrionomys* (or *Myodes*) although *Craseomys* and *Clethrionomys* are not closely related (Lebedev et al. 2007, Kohli et al. 2014). Some taxa with continuously growing molars were classified in *Eothenomys* in the past (Corbet 1978, Kaneko 1994, Suzuki et al. 2014) or were believed to represent immature *rufocanus* with dental pulps still open (Hinton 1926a, Ellerman & Morrison-Scott 1951). Tang et al. (2018) showed that the arhizodont *shanseius* nests inside otherwise rhizodont *rufocanus*. Musser & Carleton (2005) treated *Phaulomys* as a genus in its own right (with *smithii*

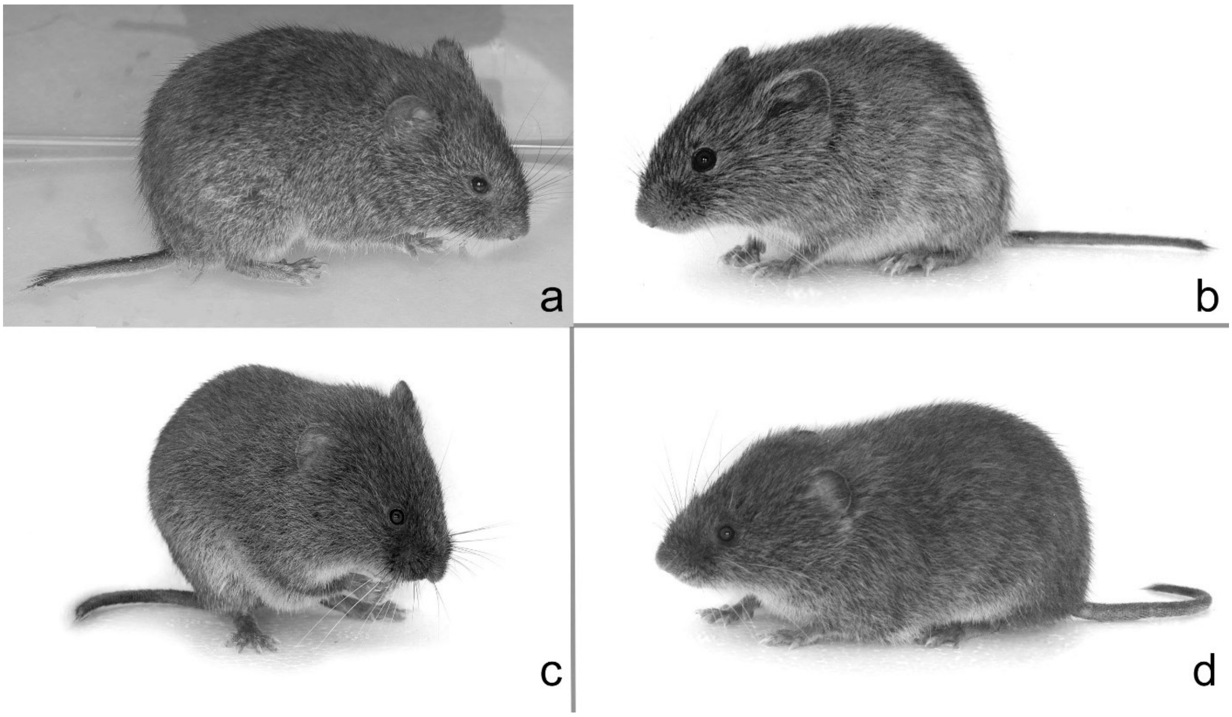


Figure 82: Grey-sided voles (*Craseomys*): a–*C. rufocanus rufocanus* (the Urals Mts., Russia); b–*C. r. bedfordiae* (Hokkaido, Japan); c–*C. smithii* (Honshu, Japan); d–*C. andersonii* (Honshu, Japan). Note that the tail is shorter in ssp. *rufocanus* (a) than in ssp. *bedfordiae* (b). Photo: Dina Nesterkova & Yuliya Davidova (a); Masahiro A. Iwasa (b–d).

and *andersoni*), but a phylogenetic reconstruction nested these species in *Craseomys* (Luo et al. 2004; Lebedev et al. 2007).

Distribution. *Craseomys* is endemic to the Palaearctic Region and all species except *rufocanus* have relatively small ranges in eastern Asia; *andersoni, smithii* and *rex* are island endemics.

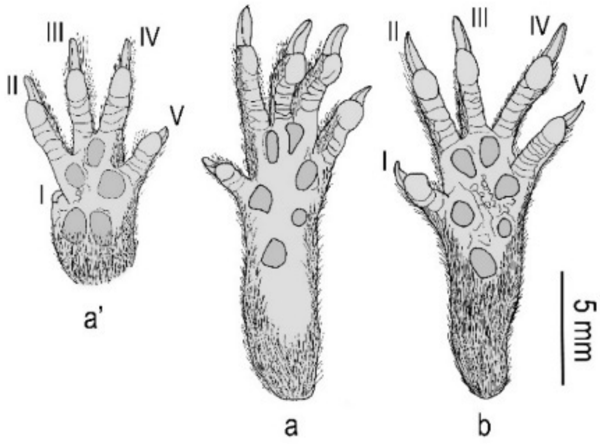


Figure 83: Left palm (a') and sole (b,c) in grey-sided voles: a–*Craseomys regulus* (Jiam-ri, South Korea) and b–*C. smithii* (Mt. Daisen, Hokkaido, Japan). Digits are indicated using Roman numerals (thumb=I).

Characteristics (Figure 82). Cranially, dentally and externally similar to *Clethrionomys*. There are 6 palmar pads and the metatarsal ones are comparatively small (Figure 83). Mammae: 2–4 pairs. In large representatives the skull is massive and angular with prominent postorbital processes and clearly defined temporal ridges. Zygomata are heavy and expand abruptly; interparietal is broad, basioccipital is narrow, and bullae are rather large. Molars are tall-crowned with distinctly alternating triangles and pointed salient angles; the formation of roots is postponed into adult age or fails entirely (in *Phaulomys*). Molar pattern depends on age in rhizodont and arhizodont grey-sided voles alike (cf. *Clethrionomys*); note that pattern is independent of age in other arhizodont Clethrionomyini (cf. *Eothenomys*; Kaneko 1996a). The enamel pattern, including the differentiation of the leading/trailing edges and the schmelzmuster, is essentially like in *Clethrionomys*. The baculum is trident with a long, narrow shaft, thus resembling *Clethrionomys* in every aspect. Diploid number of chromosomes (2n=56, $NF_a=56$) is as in *Clethrionomys*, however there are differences between these two genera in chromosomal recombination between the 1st and 9th autosomal pairs (Sokolov et al. 1990). *C. smithii* is the most aberrant member of the genus, deviating in many respects from the above description (see under the species).

Key to species

1a) Molars rooted (rhizodont) in adults 2
1b) Molars remain rootless (arhizodont) for entire life 3
2a) M³ with 2 re-entrant angles on lingual side, dental triangle T2 is usually smaller than T3; largest individuals with CbL<29.5 mm .... *rufocanus* (part)
2b) M³ with 3 re-entrant angles on lingual side, dental triangles T2 and T3 of approximately the same size; largest individuals with CbL>30 mm .... *rex*
3a) 2–3 pairs of nipples; CbL<24.5 mm .... *smithii*
3b) 4 pairs of nipples; CbL>24.0 mm 4
4a) Back yellowish brown (sandy), flanks ochraceous buff; TL/H&B<0.33 .... *rufocanus shanseius*
4b) Back dull to bright rufous, flanks grey; TL/H&B>0.33 5
5a) Dorsal mantle usually sharply defined from flanks; TL/H&B>0.50; endemic to Honshu, Japan .... *andersoni*
5b) Dorsal mantle suffused with greyish flanks; TL/H&B<0.50; endemic to Korea .... *regulus*

SUBGENUS: *Craseomys* Miller, 1900

Craseomys Miller, 1900:87. Proposed as a subgenus of *Evotomys*. Type species: *Hypudaeus rufocanus* Sundevall.

Synonyms. *Neoaschizomys* Tokuda, 1935.

This subgenus contains grey-sided voles with rooted molars; the only exception is *C. rufocanus shanseius* which is arhizodont. Results by Honda et al. (2019) question monophyly of this subgenus since *rufocanus* emerged in *Mt*-tree as a sister species to *regulus*, and not *rex*.

Craseomys rufocanus (Sundevall, 1846) – Siberian Grey-sided Vole

Taxonomy. In the past *C. rufocanus* (classified in *Aschizomys, Evotomys, Clethrionomys* or *Myodes*) encompassed various species of *Craseomys* (*andersoni, smithii, regulus*; Hinton 1926a, Ellerman & Morrison-Scott 1951) and several additional taxa which are now in *Clethrionomys* (*caesarius* and *erica*; Ellerman & Morrison-Scott 1951). Recently Tang et al. (2018) and Honda et al. (2019) demonstrated paraphyly of *rufocanus* with respect to *shanseius*. This necessitates the merging of the two taxa under a single species as done in this review. *C. shanseius* was mainly regarded as a synonym of *rufocanus* (Allen 1924, Hinton 1926a). Corbet (1978) reinstalled its species status within *Eothenomys;* Pavlinov et al. (1995) affiliated *shanseius* with *Anteliomys* (as a subgenus of *Eothenomys*), Musser & Carleton (2005) and Honda et al. (2019) with *Myodes* (=*Clethrionomys*), and Pardiñas et al. (2017) with *Craseomys*.

Arvicola kamtschatica Polyakov, 1881, is frequently synonymised with *C. rufocanus* (Corbet 1978, Musser & Carleton 2005). The dental pattern of *kamtschatica* as presented in the original description (Fig. 4 in Polyakov 1881:43) clearly points to *Alexandromys oeconomus*.

Distribution (Figure 84). Boreal forest zone (taiga) from Fennoscandia across north-eastern European Russia and Siberia to the Pacific coast. The northern border is mainly set by tundra; in the south the range extends into the southern Urals and the upper reaches of Ob, encompassing Mongolia, trans-Baikal, China (as far south as Shanxi, Hebei and Liaoning), and north-eastern North Korea. Insular populations are present on Sakhalin, Hokkaido, the Kurile Islands, Shantar, and several small islands along the coasts of Hokkaido, the mainland Far East, and in the Sea of Okhotsk (Kostenko 1984, Dokuchaev 2011). Geographic range is estimated at 13,821,700 km². *C. rufocanus* is a habitat and elevational generalist, reaching altitudes up to 3,230 m a.s.l. (Gobian Altai). Principal habitats are mesic forests and dwarf *Vaccinium* shrubs; occasionally occupies grasslands and high altitudinal tundra. Locally (e.g. the Polar Urals) depends entirely on rocky situations (screes, accumulation of boulders) on slopes (Bol'shakov 1975, Kaneko et al. 1998).

Characteristics (Figure 82a,b). Size moderately large and tail relatively short for a grey-sided vole (in mainland Eurasia TL/H&B=0.25–0.39). The reddish dorsal mantle is usually narrow and well defined against grey sides; belly is grey, shaded buff and dulled by slate underfur. There is a great deal of individual, seasonal and geographic variation in colour. Tail is sharply bi-

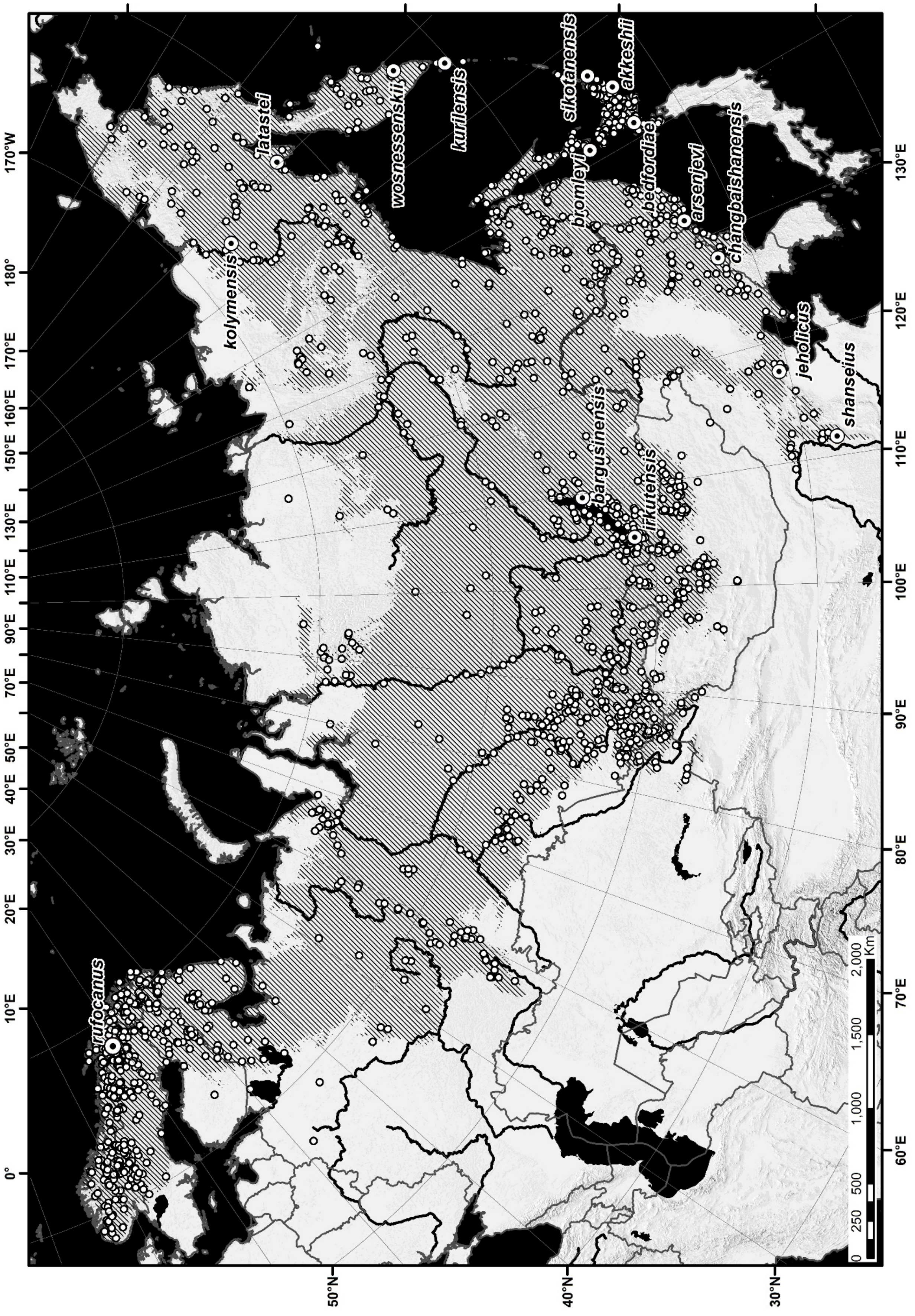


Figure 84: Distributional range of the Siberian grey-sided vole *Craseomys rufocanus*.

are greyish and the back is lightly tinted red. Females have 8 nipples. Proximal baculum in ssp. *bedfordiae* (length=2.77 mm) has narrower base (width=1.25 mm) than either *smithii* or *andersoni* (Yato & Motokawa 2021); distal trident is well-developed. Braincase is square-like (Figure 85); posterior edge of hard palate is normally interrupted, i.e. "the bridges over the lateral grooves on the posterior palate" (Thomas 1906a:354) are not complete. Formation of molar roots does not closely correlate to age and is postponed in comparison to *Clethrionomys* (Viitala 1971, Abe 1976) and *Creaseomys rex* (Borodin et al. 2012); in ssp. *shanseius*, roots do not develop at all. The M^3 usually has 2 re-entrant angles on the lingual side; the 3rd angle (LR4) is shallow and fades with age and can only be seen in young individuals (Abe 1982). Dental triangle T2 on M^3 is smaller than T3; M_1 is with 2 triangles anterior to the trigonid-talonid complex; antero-lingual T5 is usually closed, and only rarely opens into the AC (Figure 86). Karyotype (2n=56, NF_a=56–58; Orlov et al. 1978, Zima & Král 1984, Sokolov et al. 1990) shows no peculiarities except for a high proportion (1.6%) of animals with abnormalities (Kartavtseva et al. 1998).

The X is acrocentric throughout the range except in *shanseius* (submetacentric; Jiang & Ma 1991); the Y is usually small metacentric but is acrocentric in Mongolia (Orlov et al. 1978), in *bedfordiae* (Yoshida et al. 1989), and *shanseius* (Jiang & Ma 1991).

Variation and subspecies. Most of the *Cytb* heterogeneity is allocated within the south-eastern part of the range. The only widespread lineage ranges from Fennoscandia to Kamchatka while the remaining 3 lineages occupy (i) Sakhalin and Moneron Is., (ii) Hokkaido with adjacent islands (including Kunashir,

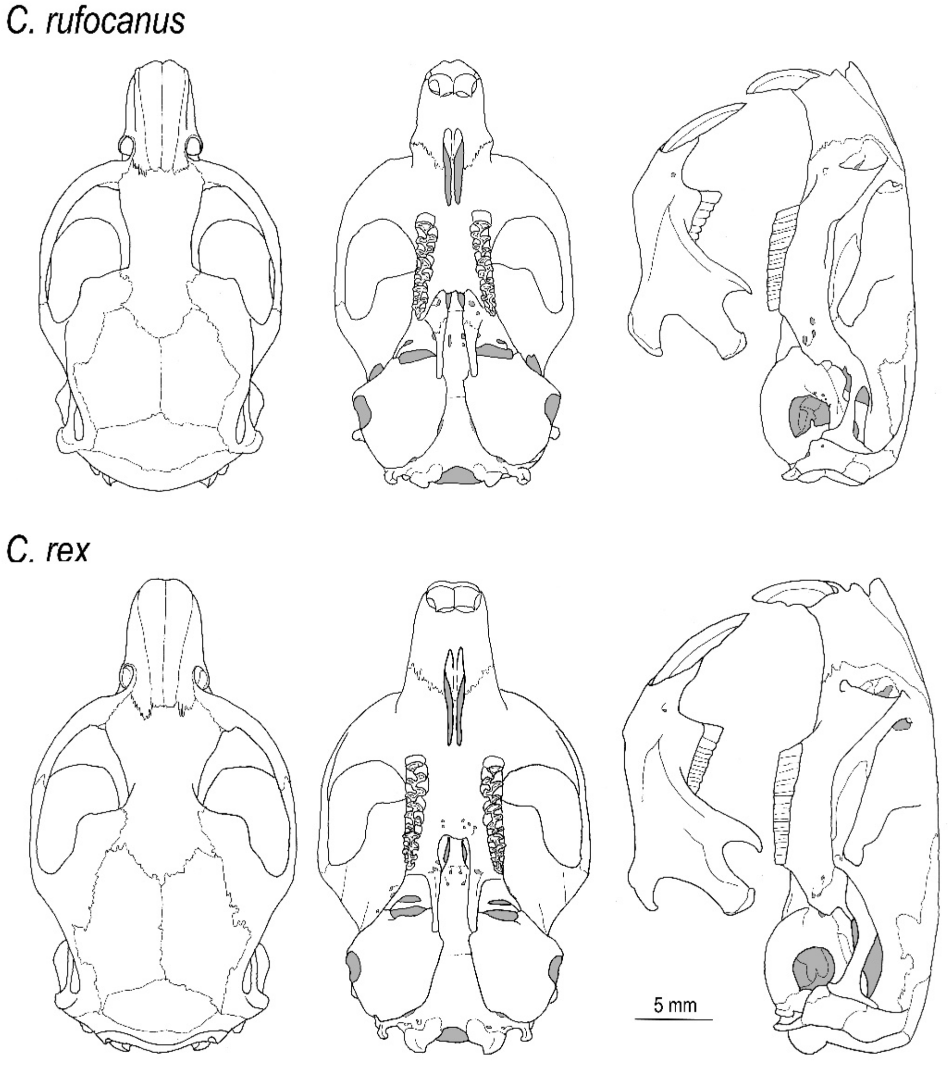


Figure 85: Skull and mandible in grey-sided voles: top–*Craseomys rufocanus* (Salla, Sundevale, Finland); bottom–*C. rex* (Shikotan Island, Kurile Isands, Russian Federation).

Rishiri, Rebun and the Kurils), and (iii) the Primorye Territory and Heilongjiang along the lower Amur River. The widespread lineage is further sub-structured and the two sublineages are separated by the Lena River; quite unexpectedly, Kamtchatkan voles belong to a lineage found to the west of the Lena River. The pattern of genetic structuring is complex, presumably as a result of repeated glacial fragmentations and subsequent expansions. Ranges of phylogenetic groups also partly overlap in contact zones and the *Sry* haplotypes do not always support mitochondrial lineages (Iwasa et al. 2000, Jin et al. 2013). Populations on several islands off Hokkaido (Teuri, Yagishiri, Rishiri, Kunashir, Daikoku) display unique haplotypes (Honda et al. 2019) and are morphologically unique (Guia & Saitoh 2011).

Approximately 5 subspecies were recognised in traditional taxonomy (Shenbrot & Krasnov 2005). Geographic trends are obvious in colouration of summer pelage which is increasingly more reddish on the back and buff along the flanks when moving towards the east (Ognev 1950). Voles from Hokkaido and Sakhalin violate this trend in having a less contrasted reddish back, longer tail, and higher proportion (4.1%) of 3rd lingual re-entrant angle on M^3 (Abe 1982). At least 2 marginal isolates are morphologically, karyologically and genetically well-differentiated and deserve to be ranked as distinct subspecies (*bedfordiae* and *shanseius*). We tentatively pooled the remaining populations under the nominal subspecies although populations in the Far East (*arsenjevi*) and in Sakhalin (unnamed) may be subspecifically distinct.

Craseomys rufocanus rufocanus (Sundevall, 1846)

Hypudæus rufocanus Sundevall, 1846:122. Type locality: “Lapponia (salten [at least] in reg. betulino-sylvatica” (p. 123); i.e. present-day Swedish Lapland (Lappmark in Miller 1900:89). Name was based on specimens from several locations: Altawaara, Karesuando, Lule, and Pite.

Synonyms. *Arvicola Wosnessenskii* Polyakov, 1881; *Arvicola rufocanus* var. *sibirica* Polyakov, 1881; *[Arvicola rufocanus]* variété *kamtschaticus* Lataste, 1884 [preoccupied by Lataste]; *Ar[vicola] Wageri* Graells, 1897 [nomen nudum]; *Evotomys (Craseomys) latastei* J. Allen, 1903 [new name for *kamtschaticus* Lataste]; *Evotomys bedfordiae* Thomas, 1905; *Evotomys kolymensis* Ognev, 1922; *Evotomys (Craseomys) irkutensis* Ognev, 1923; *Ev[otomys] ussuriensis* Ognev, 1923 [nomen nudum]; *Craseomys rufocanus bargusinensis* Turov, 1924; *Evotomys (Craseomys) arsenjevi* Dukelski, 1928; *Clethrionomys kurilensis* Kishida, 1930 [nomen nudum]; *Microtus inez jeholicus* Kuroda 1939; *Clethrionomys rufocanus* var. *karafutoensis* Tokuda,

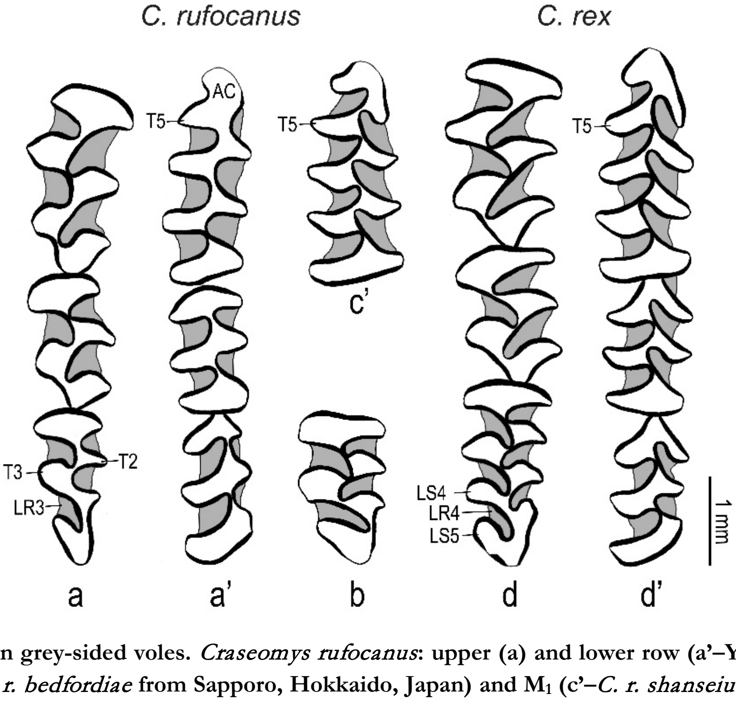


Figure 86: Molar pattern in grey-sided voles. *Craseomys rufocanus*: upper (a) and lower row (a’–Yalu Jiang River, Yichun, China); isolated M^3 (b–*C. r. bedfordiae* from Sapporo, Hokkaido, Japan) and M_1 (c’–*C. r. shanseius* from 160km north-west of Tai-Yuen-Fu, Shan-si, China). *C. rex*: upper (d) and lower row (d’–Dolinsk District, Sakhalin Island, Russian Federation).

1940 [nomen nudum]; *Clethrionomys rufocanus Changbaishanensis* Jang, Ma & Luo, 1993.

Distribution. The entire range of the species except Hokkaido, the Kuril Islands, and N China (Beijing, Shanxi and Nei Mongol).

Description (Figure 82a). Size smaller: BWt=21–52 g, H&B=91–153 mm, TL=28–57 mm, HF=16–21 mm, EL=10–18 mm, CbL=23.4–28.2 mm, ZgW=11.7–15.6 mm, MxT=5.2–7.4 mm. Tail is relatively short (TL/H&B≈0.26–0.37); M^3 usually has 2 re-entrant lingual angles. The reddish–grey contrast is usually obvious. The Y chromosome is metacentric. Despite some mosaic variations, mainland populations are remarkably uniform; e.g. Hollister (1913) stressed that specimens from the Altai Mts. were indistinguishable from Scandinavian samples.

Craseomys rufocanus bedfordiae (Thomas, 1905)

Evotomys bedfordiae Thomas, 1905a:18. Type locality: "Shinshinotsu, Hokkaido", near Sapporo, Hokkaido, Japan.

Synonyms. *Clethrionomvs rufocanus kurilensis* Tokuda, 1932; *Neoaschizomys sikotanensis* Tokuda, 1935; *N[eoaschizomys] s[ikotanensis] akkeshii* Imaizumi, 1949; *C[lethrionomys] r[ufocanus] bromleyi* Kostenko, 1984 [nomen nudum].

Distribution. Hokkaido (Japan) and adjacent offshore islands, including Kunashir and the Kuril Islands.

Description (Figure 82b). Size large: BWt=22–68 g, H&B=101–139 mm, TL=40–64 mm, HF=18–22.5 mm, EL=11–17.5 mm, CbL=25.5–29.2 mm, ZgW=14.4–16.9 mm, MxT=6.3–7.9 mm. Tail is relatively long (TL/H&B=0.35–0.64). M^3 tends towards the presence of an additional lingual re-entrant angle LR4. The reddish–grey contrast is less obvious in comparison with continental voles. The Y chromosome is acrocentric.

Craseomys rufocanus shanseius Thomas, 1908

Craseomys shanseius Thomas, 1908c:643. Type locality: "100 miles [160 km] N.W. [north-west] of Tai-Yuen-Fu, Shan-si, 8000' [2,440 m]", China.

Distribution. Beijing, Shanxi and Nei Mongol (China). Geographic range is separated from the main range by the Gobi Desert and the Manchurian plain, but connected to it through, the Greater Khingan Range. Lives among moss-grown rocks in dense spruce or larch woods at 1,650–2,450 m a.s.l.

Description. Size small: BWt=20–48 g, H&B=85–115 mm, TL=25–41 mm, HF=16–19 mm, EL=10–16 mm, CbL=23.5–28 mm, ZgW=12.8–15.6 mm, MxT=5.5–6.5 mm. Tail is distinctly short (TL/H&B=0.3–0.36). Fur is long and shaggy, greyish-rusty, sides ochraceous buff, belly light cream-buffy, clouded with slate-grey hair bases. In comparison with other populations of *C. rufocanus*, the pelage is more yellowish brown and less reddish. Tail is densely haired, dark brown above, whitish on the sides and below. Skull is small with narrow mesopterygoid fossa, very short rostrum, and a large braincase. The X chromosome is sub-metacentric and Y is acrocentric.

Craseomys rex (Imaizumi, 1971) – Dark Grey-sided Vole

Clethrionomys rex Imaizumi, 1971:99. Type locality: "Kanrosen, Mt. Rishiri, Rishiri Island, Hokkaido", Japan. **Synonyms.** *Clethrionomys microtinus* Kuzyakin, 1963 [nomen nudum]; *Clethrionomys montanus* Imaizumi, 1972.

Taxonomy. A great deal of controversy was involved in the past over the nomenclatural and taxonomic scope of *C. rex*. *Clethrionomys rex* was originally proposed as a species and either accepted as such (e.g. Corbet 1978, Kaneko 1994) or synonymised with *C. rufocanus* (Aimi 1980, Musser & Carleton 1993). Russian authors considered *rex* a species in its own right under the name *sikotanensis* but Motokawa (2008) showed that the type of *sikotanensis* is *rufocanus*. *C. rex* possibly diverged from the *rufocanus+regulus* lineage 1.59 Mya (Honda et al. 2019).

Musser & Carelton (2005) synonymised *Clethrionomys microtinus* Kuzyakin with *rufocanus*; *microtinus* was treated as a synonym of *rex* by Gromov & Polyakov (1977) and all subsequent Russian authors, a step followed here.

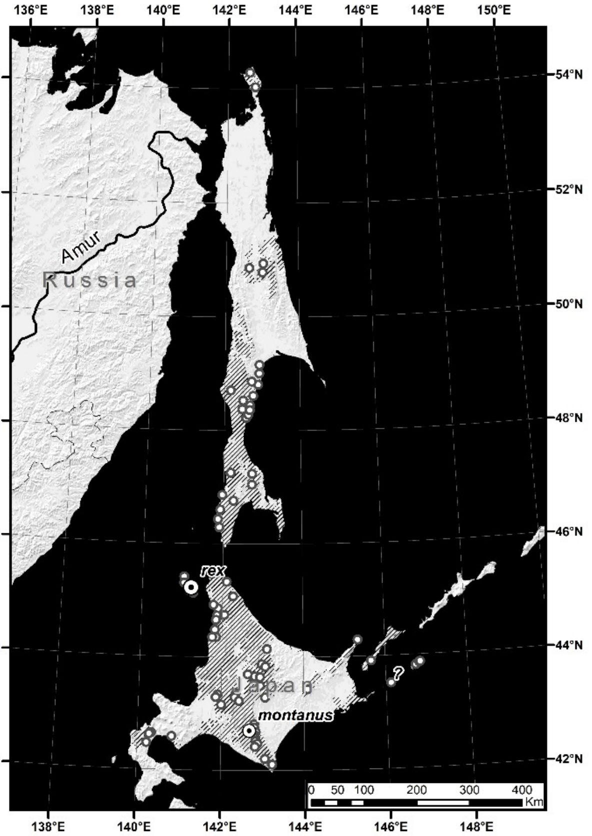


Figure 87: Distributional range of the dark grey-sided vole *Craseomys rex*.

Distribution (Figure 87). Endemic to Sakhalin, Hokkaido and smaller offshore islands: Zelenyi (=Shibotsu), Kunashir, Rebun, Rishiri) and Shikotan. Range is small (~60,200 km²) and further fragmented within each larger island. Altitudinal range is from the seashore up to 750 m in Sakhalin and 1,420 m in Hokkaido. Everywhere *C. rex* is sympatric with *C. rufocanus*; *rex* prefers grasslands, abandoned farmland, sparse *Sasa* bamboo stands and high-altitude forests, while *rufocanus* dwells in dense bamboo stands and forests. Interspecific competition for habitat is more severe on the small Rishiri Is. than on much larger Hokkaido (Iwasa & Nakata 2011). The molecular clock suggests that *C. rex* colonised Hokkaido ~0.12–0.58 Mya, i.e. earlier than *rufocanus* (0.01–0.02 Mya; Kawai et al. 2013).

Characteristics. Similar to *C. rufocanus*, but larger on average: BWt=28–87 g, H&B=103–156 mm, TL=38–68 mm, HF=18.6–24 mm, EL=12–17.5 mm, CbL=27.6–31.9 mm, ZgW=15.5–18 mm, MxT=7–8.4 mm. Back is darker and brown and flanks are less grey. Underside is grey with buff wash. Fur is short; paws and ears are grey; tail is nearly black above, indistinctly bi-coloured and has a short terminal pencil. Females have 8 nipples. Baculum (reported as *rufocanus*; Anderson 1960) is like in *rufocanus* except that median digit has a proximal notch. Skull is robust and ridged (Figure 85), posterior edge of hard palate is normally interrupted behind the posterior palatine vacuity (Kostenko 1984, Kaneko et al. 1998). M^3 is with 3 re-entrant angles on the lingual side; dental triangle T2 is of approximately the same size as T3 (Figure 86d). Karyotype (2n=56, NF_a=56) as in *rufocanus*, except that the Y chromosome is acrocentric (due to a pericentric inversion) in the majority of populations (Yoshida et al. 1989, Sokolov et al. 1990, Iwasa & Suzuki 2002a), and rarely submetacentric (Iwasa & Nakata 2015).

Variation and subspecies. Monotypic. Voles from Sakhalin and Kunashir have longer skulls on average (mean=29.3 mm) than those from Shikotan (27.2 mm). Four allopatric *Mt*-lineages were retrieved on Hokkaido, presumably reflecting range fragmentation since the Middle Pleistocene (Kawai et al. 2013). Populations from Rishiri and Rebun Islands have exclusive *Cytb* haplotypes (Iwasa & Nakata 2011, Honda et al. 2019).

SUBGENUS: *Phaulomys* Thomas, 1905

Phaulomys Thomas, 1905c:493. Proposed as a subgenus of *Evotomys*. Type species by monotypy: *Evotomys smithii* Thomas.

Taxonomy. *Phaulomys* contains 3 species (*andersoni, smithii* and *regulus*) with permanently rootless (arhizodont) molars which evolved along the south-eastern distributional margin of *Craseomys*. Aoki (1913) was perhaps the first to include *Phaulomys* in *Craseomys* and his taxonomic setting was recently reconfirmed by chromosomal and molecular markers (Iwasa & Tsuchiya 2000, Luo et al. 2004, Lebedev et al. 2007).

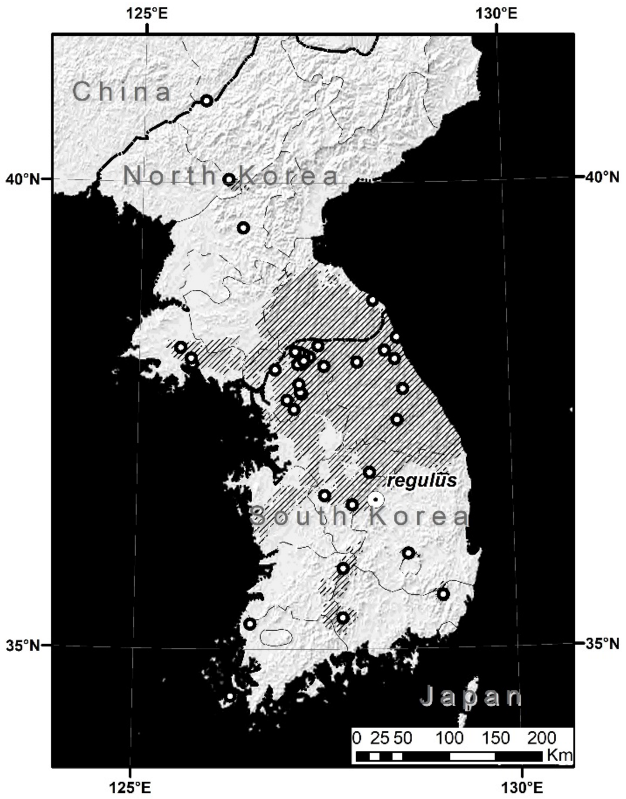


Figure 88: Distributional range of the Korean grey-sided vole *Craseomys regulus*.

Craseomys regulus Thomas, 1907 – Korean Grey-sided Vole

Craseomys regulus Thomas, 1907a:863. Type locality: "Min'gyongl [= Mun'gyong; Jones & Johnson 1965], 110 miles [177 km] S.E. of Seoul. Alt[itude]. 1100–1300 ft. [335–400 m]", South Korea.

Taxonomy. Although described as a species in its own right, *C. regulus* was subsequently classified as a subspecies of *Evotomys rufocanus* (Allen 1924, Howell 1929, Won 1968). Many authors (e.g. Corbet 1978, Kaneko 1990) recognised *regulus* as a species of *Eothenomys*, and Pavlinov et al. (1995) affiliated it with *Caryomys* (a subgenus of *Eothenomys*). *Craseomys regulus* differs from the Korean *rufocanus* due to its brighter back, more buffy and less greyish underparts, longer tail (TL/H&B=0.26–0.37), larger skull, broader rostrum, wider interorbital region (3.9–4.7 mm in *regulus* vs 3.2–4.1 mm in *rufocanus*; Kaneko 1990), shorter molar-row, and larger bullae (Jones & Johnson 1965). Species status of *regulus* was supported in molecular phylogenetic reconstructions (Koh et al. 2010, 2011, Tang et al. 2018). Misidentifications of *C. rufocanus* as *C. regulus* are common in older literature (e.g. Allen & Andrews 1913, Hinton 1926a, Howell 1926, Tokuda 1941). Taxonomic and geographic scope of *regulus* is defined in Kaneko

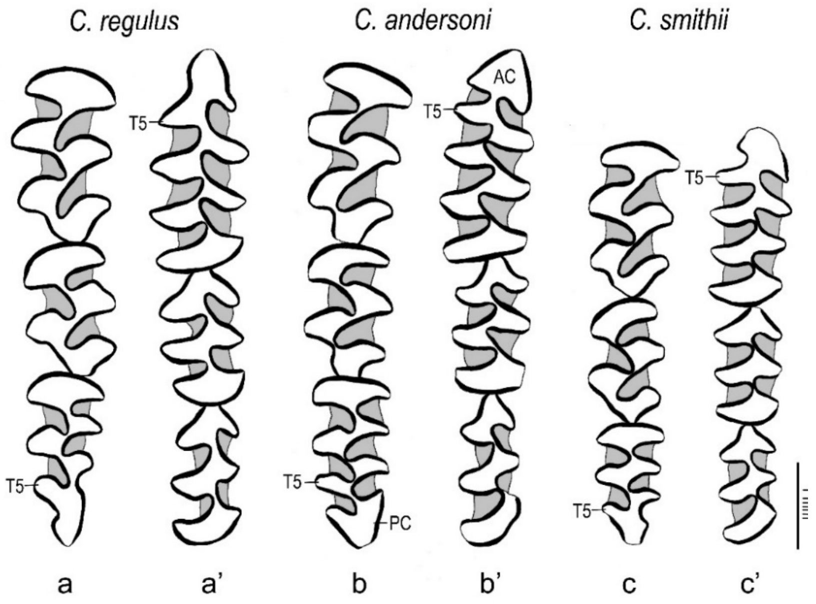


Figure 89: Molar pattern in grey-sided voles (subgenus *Phaulomys*). Pictured are upper (a,b,c) and lower rows (a',b',c') in (left to right) *Craseomys regulus* (from Sokwang-sa, North Korea), *C. andersoni* (Minami Alps, Yamanashi Prefecture, Honshu, Japan), and *C. smithii* (Nagano Prefecture, Honshu, Japan).

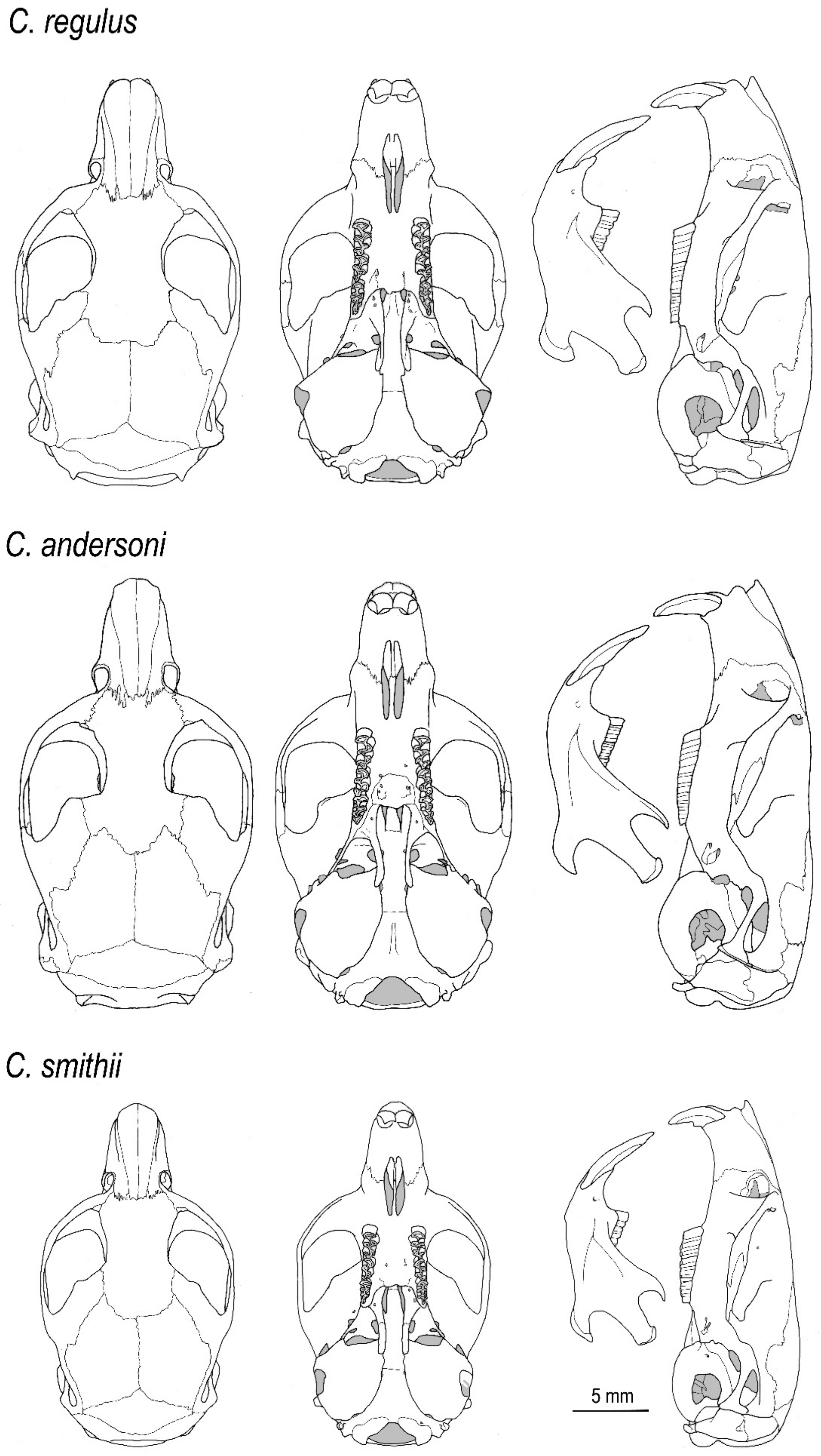


Figure 90: Skull and mandible in grey-sided voles (subgenus *Phaulomys*): top–*Craseomys regulus* (Mun'gyong, Seoul, South Korea); middle–*C. andersoni* (Iwate Prefecture, Honshu, Japan); bottom–*C. smithii* (Nagano, Kiso, Japan).

(1990). In *Cytb* phylogenetic reconstruction by Honda et al. (2019), *regulus* is a sister species to *rufocanus* and the two putatively diverged 1.02 Mya.

Distribution (Figure 88). Endemic to Korea, south of ~41⁰ northern latitude. Habitat modelling suggests contiguous range only for the central parts of the peninsula. Range is small (64,276 km²) and further fragmented in its northern and southern parts. Altitudinal range is from the seashore up to 1,730 m, but mainly inhabits lowlands. Preferred are habitats with abundant stone coverage and little ground vegetation cover (Lee et al. 2022).

Characteristics. Moderately large grey-sided vole: BWt=21–38 g, H&B=91–120 mm, TL=35–48 mm, HF=16.5–21 mm, EL=9–15.5 mm, CbL=23.9–27.9 mm, ZgW=13.1–14.5 mm, MxT=6–6.8 mm. The tail (TL/H&B=0.35–0.45) is longer than in *rufocanus* but shorter in comparison to *andersoni*; it is densely clothed and sharply bi-coloured (brown above, cream buff below). Summer fur is coarse; winter hair is long (8–9 mm) and soft. Back is cinnamon-brown to cinnamon-rufous or intense hazel. The mantle is barely defined, flanks are lighter and the belly is greyish-white to grey, washed fulvous to buff. Young animals are decidedly darker. Females have 8 nipples. Skull as in *rufocanus*, except for a longer and more ovate braincase (Figure 90); zygomatic arches are moderately bowed (ZgW/CbL=0.55–0.61). Molars are rootless for the entire lifespan and display a prominent alveolar cusp; M³ has 3–4 re-entrant angles on both sides (Figure 90a). Karyotype: 2n=56, both heterosomes are subtelocentric (Iwasa et al. 1999a, Iwasa & Suzuki 2002a).

Variation and subspecies. Monotypic species.

Craseomys smithii (Thomas, 1905) – Smith's Grey-sided Vole

Evotomys (Phaulomys) Smithii Thomas, 1905e:493). Type locality: "Kobe, Hondo [= Honshu], Alt. 650 m" (p. 495), Japan.

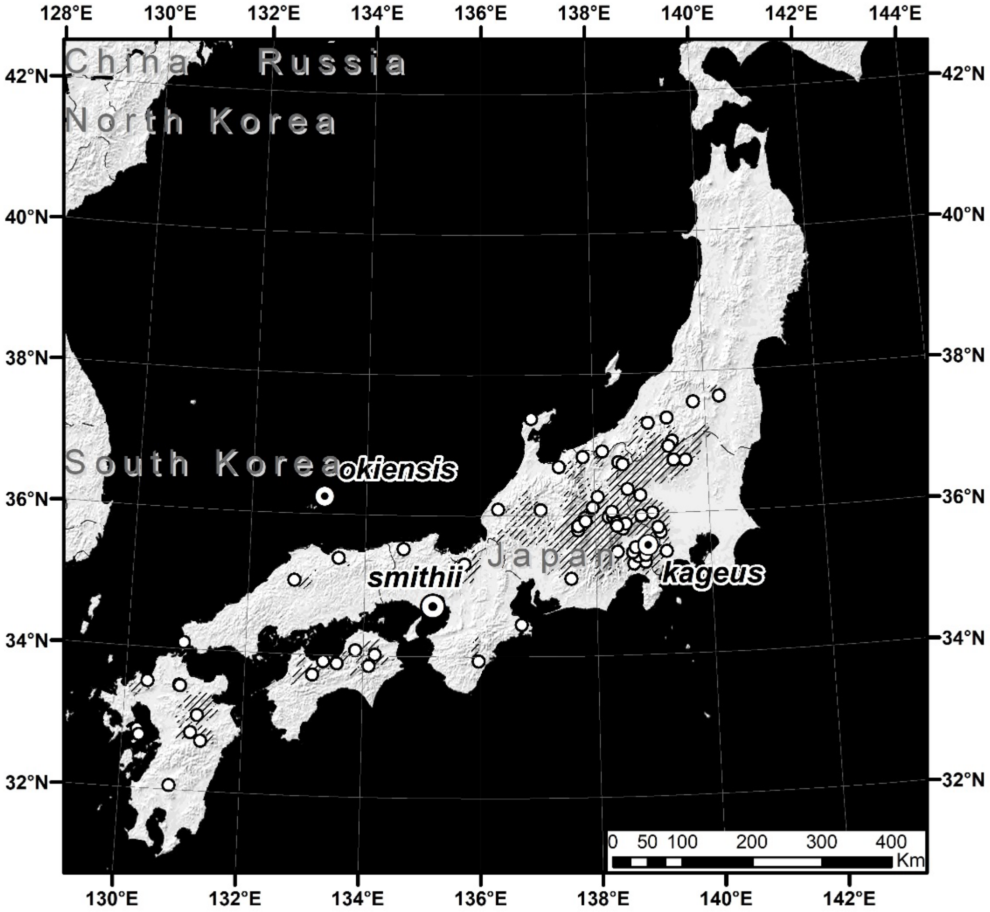


Figure 91: Distributional range of Smith's grey-sided vole *Craseomys smithii*.

Synonyms. *Clethrionomys rufocanus okiensis* Tokuda, 1932; *Eothenomys kageus* Imaizumi, 1957.

Taxonomy. *C. smithii* was described as a full species but was subsequently synonymised with *C. rufocanus* (Kuroda 1938, Ognev 1950, Ellerman & Morrison-Scott 1951) and was classified to one of the following genera: *Eothenomys* (Imaizumi 1949, Corbet 1978), *Clethrionomys* (Tokuda 1941, Ellerman & Morrison-Scott 1951), *Aschizomys* (Gromov & Polyakov 1977) or *Myodes* (Musser & Carleton 2005). Differentially stained (G-bands) karyotype (Iwasa & Tsuchiya 2000) and molecular evidence (Lebedev et al. 2007) retrieved *smithii* as a member of *Craseomys*. Ognev (1950) also included *bedfordiae* and *andersoni* (with *niigate*) in *smithii*. Earlier authors regarded the number of nipples to be of taxonomic significance; Jameson (1961) distinguished 2 species on this ground, *smithii* (6 nipples) and *kageus* (4 nipples).

C. smithii differs from sympatric *andersoni* in smaller size, shorter tail, a unique molar pattern and in details of cranial structure: in *smithii* the lateral projection of the lambdoidal crest is more prominent, the middle lacerate vacuity is more elliptical (more slit-like in *andersoni*), and the inner margins of the tympanic bullae are shifted wider apart (Iwasa 2000). Molecular (Fujimoto & Iwasa 2010, Honda et al. 2019) and karyological evidence (Iwasa et al. 1999b) suggests geographically restricted past introgression between *smithii* and *andersoni*.

Distribution (Figure 91). Endemic to Japan, specifically to Honshu (except its northern portion), Shikoku, Kyushu and the Dogo Is. (Oki island group). Total range is estimated at 43,785 km^2. Mesic forests at 60–2,400 m a.s.l. are the preferred habitat.

Description (Figure 82c). A small species of *Craseomys:* BWt=18–35 g, H&B=90–115 mm, TL=38–54 mm, HF=15–18.5 mm, EL=10–16 mm, CbL=21.8–24.4 mm, ZgW=12.3–14.4 mm, MxT=5.3–6.4 mm. Tail is moderately long (TL/H&B=0.34–0.65), well-haired and with a distinct terminal pencil. Fur is soft and loose (length ~10 mm), light russet-brown to dull brown above, lighter on flanks and cream-buff below; hair bases are slate. Pelage lacks reddish tone and flanks do not abruptly turn grey as is common in the genus. Mammae: 4 (all inguinal) or 6 (4 inguinal+2 pectoral); nipple count can be asymmetrical (=5); estimated average=5.1 (n=47). Pectoral nipples are either normally developed or retarded in size, but always lack mammary tissue (Kaneko 1985). Proximal baculum is 2.72 mm long and 1.49 mm wide (Yato & Motokawa 2021). Skull deviates from the general condition of *Craseomys* in its delicate and rounded structure with barely developed postorbital projections (Figure 90); zygomatic arches widely spread (ZgW/CbL=0.55–0.6); auditory bullae are small. The molar pattern tends to be smooth rather than angular. M^3 is either simple (with 2 lingual re-entrant angles) in ~$^1/_3$ of individuals, or complex (with 3 inner re-entrant angles); the proportion of simplex type increases with advanced age (Kaneko 1996a). Karyotype: 2n=56, NF_a=56; X is subtelocentric, Y is small subtelocentric (Yoshida et al. 1989, Iwasa & Suzuki 2002a).

Variation and subspecies. Individual heterogeneity blurs the geographic variation and no subspecies were recognised on morphological grounds. Voles are on average smaller in the south and larger in the north but differences are slight. The Shikoku population possess unique *Cytb* haplotypes (Iwasa & Suzuki 2002b).

Craseomys andersoni (Thomas, 1905) – Anderson's Grey-sided Vole

Evotomys (Craseomys) andersoni Thomas, 1905a:18. Type locality: "Tsunagi, N.[orthern] Hondo"; subsequently fixed at "Northern Hondo [= Honshu], near Morioka" (Thomas 1905b:354), Iwate Prefecture, Japan.

Synonyms. *Craseomys niigate* Anderson, 1909; *Clethrionomys imaizumii* Jameson, 1961.

Taxonomy. In the past *andersoni* was classified in different genera: *Evotomys* (Thomas 1905a), *Craseomys* (Aoki 1913), *Clethrionomys* (Kuroda 1938, Imaizumi 1949, Corbet 1978), *Aschizomys* (Imaizumi 1960, 1979), *Phaulomys* (Pavlinov et al. 1995), *Eothenomys* (Abe 2007), and *Myodes* (Honda et al. 2019). The name itself was either synonymised with *Evotomys* (or *Clethrionomys*) *rufocanus smithii* (Hinton 1926a, Ellerman & Morrison Scott 1951) or *Cl. rufocanus bedfordiae* (Kuroda 1938). Imaizumi (1949) classified *andersoni* as a subspecies of *rufocanus*. A further two names, *niigate* and *imaizumii,* were kept as distinct species in the past (Aoki 1913, Jameson 1961, Imaizumi 1979) but have been merged with *andersoni* since the late 1970s; Musser & Carleton (2005), however, reinstalled *imaizumii* as an independent species.

Distribution (Figure 92). Endemic to Honshu (Japan) where they are confined to the central and northern parts of the island as far west as the Kii Peninsula. Distribution area measures 40,787 km² and the range is fragmented. *C. andersoni* is an elevational generalist, ranging from sea level to the alpine zone (up to 2,870 m) but avoids sympatry with *smithii*. It is less resistant against water shortage stress than *smithii* (Kitahara 1993).

Characteristics (Figure 82d). Externally resembles *C. rufocanus bedfordiae* but the tail is longer (TL/H&B=0.48–0.68). Dimensions: BWt=23–45.3 g, H&B=103–135 mm, TL=58–80 mm, HF=17.5–21.4 mm, EL=12–15.5 mm, CbL=24–28 mm, ZgW=13.3–15.8 mm, MxT=6–7.3 mm. Back is clear brown, lined chestnut in some individuals, lightening gradually along the flanks; belly is slate grey and frequently washed buff. Young animals are greyish brown. Females have 8 nipples. Proximal baculum is 2.79 mm long; bacular base (width=1.65 mm) is wider than in *C. smithii* (Yato & Motokawa 2021). Skull as in *rufocanus* but more lightly built, the interorbital region tends to be concave; the bridges over the lateral grooves on the posterior palate are complete (Figure 89). Incisors and molars are narrower than in *rufocanus*. Enamel pattern shows no particulars; M^3 has 3 inner re-entrant angles (Figure 89b). Karyotype: 2n=56, NF_a=56; X is acrocentric, rarely subtelocentric; Y is small metacentric or subtelocentric (Yoshida et al. 1989, Iwasa & Suzuki 2002a).

Variation and subspecies. Size varies with large voles in the Kii Peninsula (*imaizumii*) and small voles in the northern Honshu. The population isolate in the Kii posses unique haplotypes for *Cytb* (Honda et al. 2019) and shows high polymorphism for *Sry* haplotypes (Iwasa & Suzuki 2002b). Voles from Kii produced fertile hybrids with *andersoni* in captivity (Kitahara & Kimura 1995). Monotypic species.

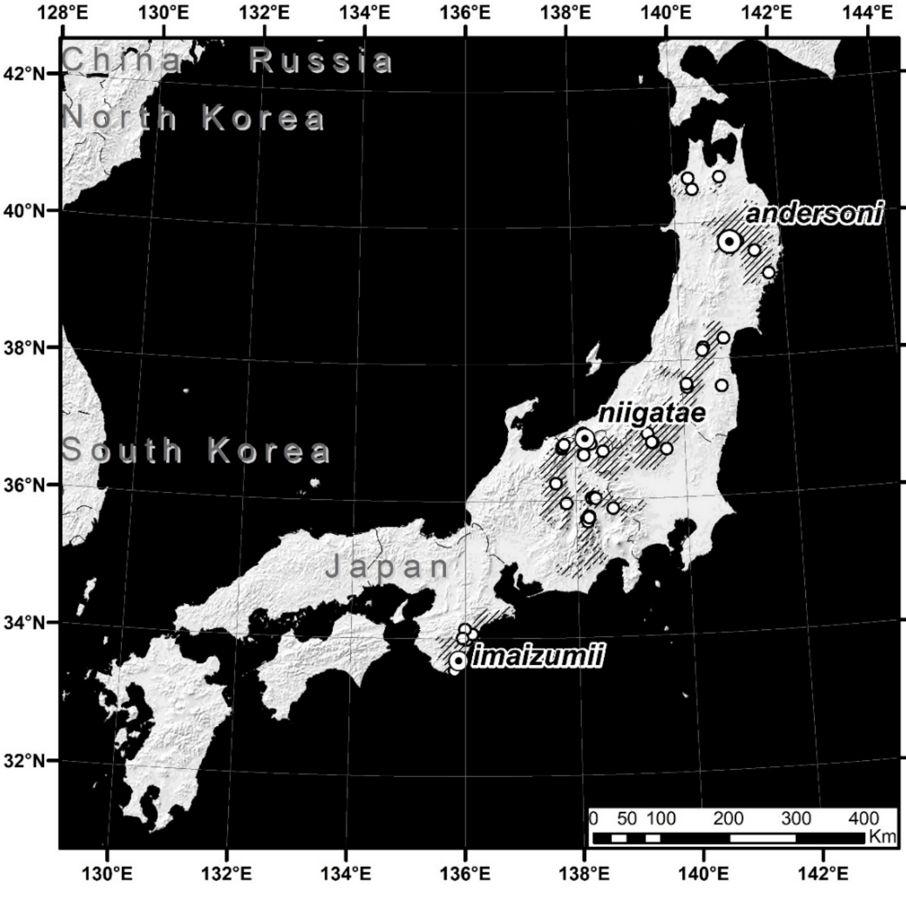


Figure 92: Distributional range of Anderson's grey-sided vole *Craseomys andersoni*.

SUBTRIBE:
Eothenomyina – New Subtribe

Nomenclature. Ye et al. (2000) introduced Eothenomi but only in the English abstract to their paper on p. 181. Nowhere is the name presented as a new family-group name and we suppose that Eothenomi is the incorrect subsequent spelling of *Eothenomys*. Eothenomi is not available for nomenclatural purposes.

Diagnosis and Comparisons. Sister group to Clethrionomyina as evident from a multigenic phylogenetic reconstruction based on nuclear and *Mt*-genes (Cyt*b, COI,* and *GHR* in Tang et al. 2018; Cyt*b, BRCA1, GHR, Rbp3*, and *RAG1* in Steppan & Schenk 2017). Morphology and karyology (2n=32, 54, 56) indicate different evolutionary trajectories between Clethrionomyina and Eothenomyina despite a partial overlap in character states. In Eothenomyina, pelage is usually dull brown with a bronzy reflection or a grizzled ("frosty") appearance (frequently rusty or grey in Clethrionomyina). Females have 4 nipples (usually 8 in Clethrionomyina). Skull is heavily built with prominent temporal ridges, lambdoidal crest and postorbital (squamosal) process (lightly built and weakly ridged in Clethrionomyina); interorbital region is wide (usually constricted in Clethrionomyina). Upper incisors usually have a shallow longitudinal groove (smooth in Clethrionomyina); molars are rootless (rooted in *Clethrionomys* and several species of *Craseomys)*. Dental fields of opposing triangles of various molars (most notably of M_1) are frequently confluent (usually alternate in Clethrionomyina); M^2 has additional postero-lingual salient angle LS4 (T5) in several genera (never seen in Clethrionomyina); LS4 is rarely also present in M^1. M^3 attains greater complexity (up to 5 inner salient angles) than Clethrionomyina (up to 4 lingual salient angles).

Distribution. Predominantly a group of the Palaearctic-Oriental transitional zonegroup; its range only marginally overlapps Clethrionomyina in the Qinling (Qin) Mts. south of the Loess Plateau and the Huang He River; only *Caryomys inez* slightly transgresses the Huang He.

Type genus. *Eothenomys* Miller, 1896.

Content. Contains 3 genera (*Caryomys, Eothenomys*, *Anteliomys*) with 12 species (see below).

GENUS: *Caryomys* Thomas, 1911 – Brownish Voles

Caryomys Thomas, 1911a:4. Type species: "*M[icrotus] inez* Thos."

Taxonomy. *Caryomys* was established as a subgenus of *Microtus* and was long regarded as being "nearly annectant between the red-backed mice of the genus *Clethrionomys* and *Microtus* proper" (Allen 1940:832). A competing view interpreted all taxa of *Caryomys* to be immature *Craseomys rufocanus shanseius* (Hinton 1926a, Ellerman 1941). Because of its arhizodont molars, *Caryomys* was frequently included into *Eothenomys* (Corbet 1978, Corbet & Hill 1992, Kaneko 1992, McKenna & Bell 1997), often as its subgenus. Gromov & Polyakov (1977) continued to regard *Caryomys* as part of *Clethrionomys* (which also included *Craseomys*) and several authors ignored the name entirely (e.g. Simpson 1945). Using chromosomal evidence, Ma & Jiang (1996) restored *Caryomys* as a genus in its own right, confirmed by molecular evidence; *Caryomys* is in a sister position against *Eothenomys*+*Anteliomys* (Liu et al. 2012a, Tang et al. 2018).

The vernacular name "brownish voles" was used for *Caryomys* as early as by Allen (1940).

Distribution. Endemic to central China south of Inner Mongolia. Ranges of the two species partly overlap, however, *C. inez* gravitates towards northern China, and *C. eva* towards western China. In addition, these species segregate habitat along the humidity gradient: *C. inez* prefers dry habitats and *C. eva* occupies humid environments (Li & Xue 2008). Both species were sympatric in faunas from the Middle and Upper Pleistocene (Li & Xue 2009). During the Middle Pleistocene, the range extended further north into Anhui Province (Tong et al. 2018).

Characteristics. Small and slender fossorial voles, externally resembling *Eothenomys*. The pelage, however, is long and soft in *Caryomys* (more velvety in *Eothenomys*). Tail is of variable length (TL/H&B=0.29–0.72) and sparsely clad with hairs which do not conceal the annulation; the terminal pencil is short. The ears are rounded and short, not protruding above the hair. Hind foot has 6 plantar pads; females have 4 inguinal nipples.

The skull is essentially as in *Eothenomys*: zygomatic arches are widely expanded (ZgW/CbL=0.55–0.62), interorbital region is markedly broad and the entire skull is deep. Auditory bullae have no internal spongy tissue. Bony palate terminates in a simple transverse bony shelf; its posterior border is at the level of the anterior loop of M^3 and is complete (Figure 10d). The presphenoidal bone is long and narrow. Bullae are of average size; incisive foramina are moderately long (barely reaching the level of M^1) and their borders are convex (Figure 93). Incisors are narrow; the upper incisors have a shallow longitudinal groove which is shifted laterally. Molars are rootless. Enamel pattern resembles conditions found for *Craseomys* except that the outer prisms are more sharply angular and nearly all triangles are closed. Salient angles are abundantly filled with cement. M_1 normally has 5 inner and 4 outer salient angles; M^3 has 3–4 lingual and 3 buccal salient angles; additional salient angles are occasionally present but are never prominent (Figure 94). Karyotype: 2n=54 (Ma & Jiang 1996).

Key to species

1a) TL/H&B<0.47; adult skull smooth; posteroconid complex longer than the anterior part of M^3; M_1 occasionally with a shallow lingual re-entrant angle LR5 .... *inez*

1b) TL/H&B>0.47; adult skull moderately angular; posteroconid complex shorter than the anterior part of M^3; M_1 lacks lingual re-entrant angle LR5 .... *eva*

Caryomys inez (Thomas, 1908) – Short-tailed Brownish Vole

Distribution (Figure 95). The entire range is estimated at approximately 76,700 km² and encompasses Shaanxi, Shanxi, Hebei, Henan, Ningxia, and eastern Gansu; there is an isolate in the Dabie Shan Mts. (Anhui near the Hebei border; Zhang et al. 1997). Habitat is semi-dry broadleaf woodland, brushwood, clearings and farmland in hilly regions (870–2,500 m a.s.l.), chiefly on both sides of the Yellow River. The region has a mean annual temperature of 8–14^0 C and receives precipitation of 390–450 mm annually (Li & Xue 2008).

Description. A short-tailed (TL/H&B=0.29–0.46) brownish vole with a long posterior cap on M^3. Fur is of varying shades of brown; for details see subspecies section below. The skull is delicately built and remains smooth with advanced age (Figure 93); zygomatic arches are fairly widely bowed (ZgW/CbL=0.56–0.62). M^3 with 3–4 salient angles on either side; a rudimentary postero-labial triangle (T6) is frequently present; the posterior cap is elongated. M_1 often has an additional re-entrant angle LR5 on the lingual side (Li & Xue 2009). Karyotype (2n=54, NF_a=60) contains 6 pairs of metacentric and 2 pairs of subtelocentric autosomes; the X is subtelocentric and the Y is telocentric (Ye et al. 2002).

Variation and subspecies. The majority of authors agree that *inez* contains two subspecies (e.g. Allen 1940, Zhang et al. 1997, Wang 2003); their geographic ranges are mapped in Luo et al. (2000:467).

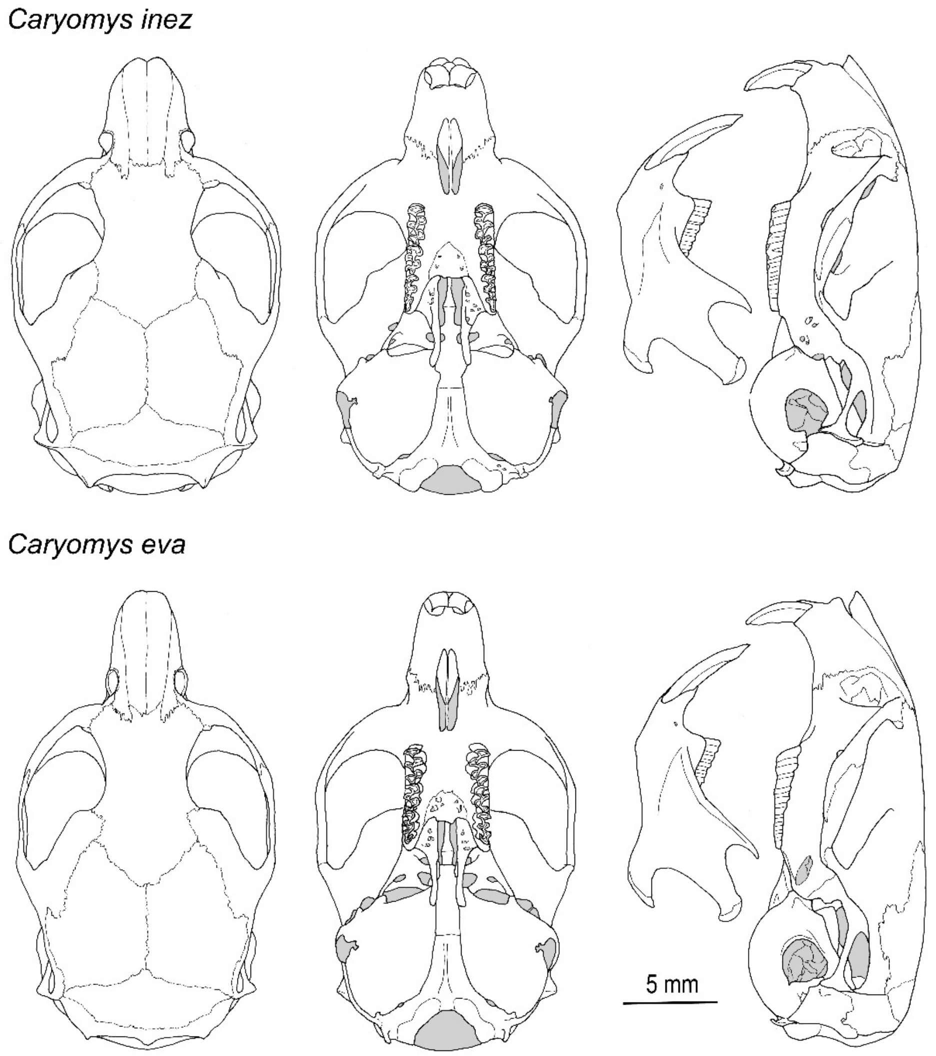


Figure 93: Skull in brownish voles: top–*Caryomys inez* (Kolanchow, Shanxi, China); bottom–*C. eva* (Taochow, Gansu, China).

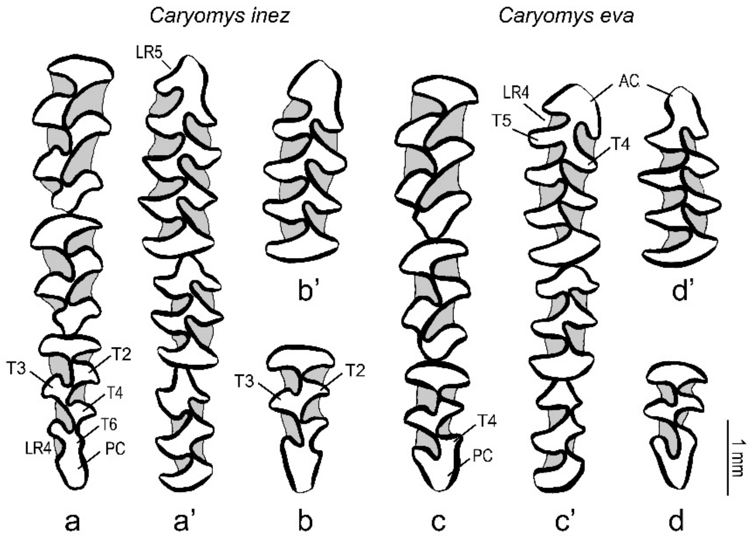


Figure 94: Molar pattern in brownish voles (all from China). *Caryomys inez inez*: upper (a) and lower row (a'–Kolanchow, Shanxi). *C. inez nux*: isolated M$_1$ (b') and M^3 (b–both from Shang Xian, Shensi). *C. eva alcinous*: upper (c) and lower row (c'–Wenchuan Xian, Szechuan). *C. eva eva*: isolated M$_1$ (d') and M^3 (d–Taochow, Gansu).

Caryomys inez inez (Thomas, 1908)

Microtus (Eothenomys) inez Thomas, 1908b:45. Type locality: "Mountains 12 miles [19km] N.W. [north-west] of Ko-lan-chow [Kolanchow], Shan-si [Shanxi]. 7000' [2,135m]" (Thomas 1909a:976).

Distribution. Southern Hebei, Shanxi, western Henan, western Anhui, northern and central Shaanxi.

Description. Dimensions: BWt=18–27.4 g, H&B=85–110 mm, TL=30–38 mm, HF=14.5–17 mm, EL=9–13 mm, CbL=21.9–24.5 mm, ZgW=12.7–14.7 mm, MxT=5.0–6.0 mm. Tail on average shorter (TL/H&B=0.34–0.42) and zygomatic arches more expanded (ZgW/CbL=0.56–0.62); bullae are smaller. Pelage is lighter: back is dull ochraceous buff, mixed with brown-tipped hairs, darker on the head; underside is light whitish, washed buff and clouded by slate hair bases. Feet are dull whitish; tail is indistinctly bicoloured, brown above, lighter below.

Caryomys inez nux (Thomas, 1910)

Microtus (Eothenomys) nux Thomas, 1910a:26. Type locality: "Shang-chou [Shang Xian, Kaneko 1992]; S.E. [south-eastern] Shen-si [Shensi]. 3300' [1,000 m]" (Thomas 1910:636).

Distribution. South-western Shaanxi, Ningxia, Gansu, and possibly northern Sichuan (Wang 2003).

Description. Dimensions: BWt=17–32 g, H&B=87–109 mm, TL=32–43 mm, HF=14–17 mm, EL=8–12 mm, CbL=22.7–24.6 mm, ZgW=12.9–14.5 mm, MxT=5.1–5.9 mm. Tail on average longer (TL/H&B=0.39–0.46) and zygomatic arches less expanded (ZgW/CbL=0.57–0.59); bullae are larger. Pelage duller than in the previous subspecies: back is deep brownish-ochraceous with a ruddy shine; flanks are similar but lack a rusy tint and the underside is brown with buffy wash; hair bases are invariably slate. Feet are dull whitish or light brown; tail is indistinctly bi-

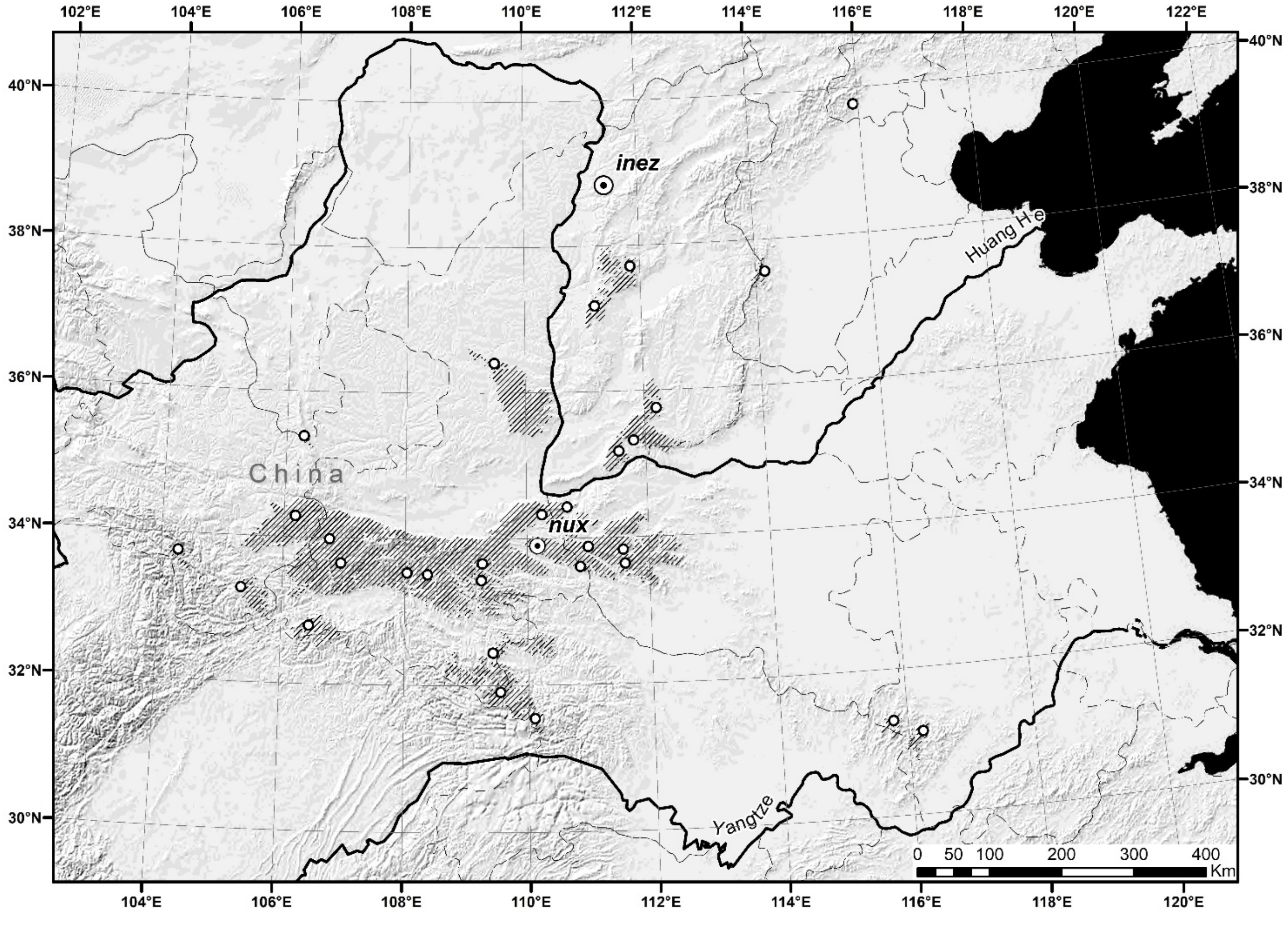


Figure 95: Distributional range of the short-tailed brownish vole *Caryomys inez*.

coloured, dark brown or blackish above, dull whitish below. M³ has confluent dental fields T2–T3 (isolated in ssp. *inez*); M_1 frequently has confluent T4–5 (pitymoyd morphotype) (Figure 94b,b').

Caryomys eva (Thomas, 1911) – Long-tailed Brownish Vole

Distribution (Figure 96). Central China in Gansu, Qinghai, Ningxia, Sichuan, Shaanxi, and Hubei. The entire range covers an estimated 94,118 km². *C. eva* occupies higher altitudes (1,350–3,400 m) on both sides of the Qinling Mts. in warm and humid forests (deciduous and coniferous), having 600–1,200 mm of precipitation annually (Li & Xue 2008, Sheftel et al. 2017).

Description. General appearance and fur texture as in *inez*, but distinguishable at a glance by its long tail (TL/H&B=0.55–0.58). Fur is of varying shades of brown but colour varies geographically; see under subspecies. Glans penis is cylindrical, 4.1–4.4 mm long and 1.9–2.0 mm wide. Baculum has ossified trident; the proximal baculum is 0.4 mm long and 1.3–1.4 mm wide at the base; the medial distal baculum is 1.4–1.7 mm long (Yang et al. 1992). Skull is delicately constructed, however the suprorbital ridges are well developed and extend onto the temporal region (Figure 93). Zygomatic arches are moderately expanded (ZgW/CbL=0.55–0.58); posterior palate edge is slightly bowed rather than straight. M³ with 3 salient angles on the lingual and labial side; the posterior cap is short. M_1 lacks re-entrant angle LR5 on the lingual side (Li & Xue 2009); the anterior loop is simple, oval or arrow-headed (Figure 94c,d). Karyotype (2n=54, NF_a=56) consists of 2 pairs of metacentric and 2 pairs of subtelocentric autosomes; the X is metacentric and the Y is telocentric (Ye et al. 2002).

Variation and subspecies. The majority of authors accept 2 subspecies (e.g. Allen 1940, Zhang et al. 1997, Wang 2003) which are separated by the Minjiang River.

Caryomys eva eva (Thomas, 1911)

Microtus (Caryomys) eva Thomas, 1911a:4. Type locality: "Near Tau-chow, Kansu"; amended to "Mts. S.E. [south-east] of Tau-chow [Taochow], Kan-su [Gansu], 10,000' [3,350 m]" (Thomas 1911d:175).

Synonyms. *Craseomys aquilus* G. M. Allen, 1912.

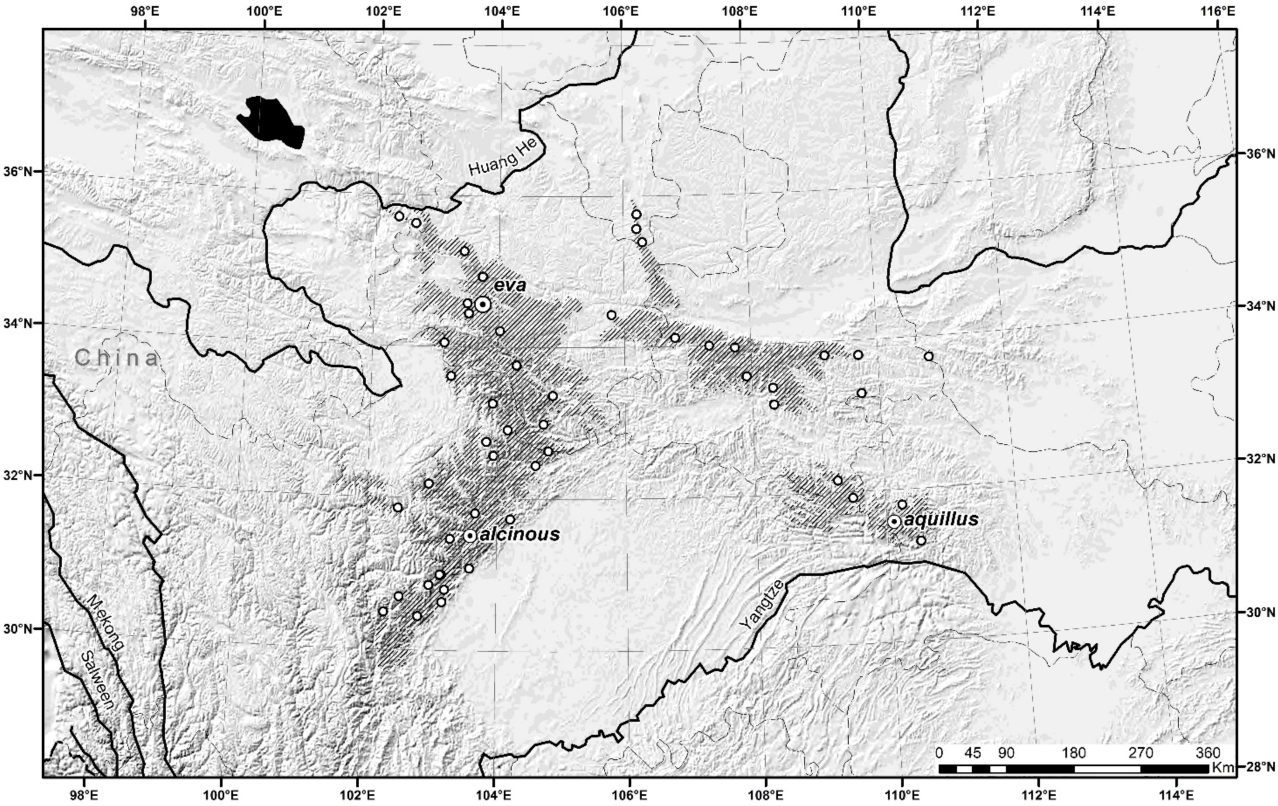


Figure 96: Distributional range of the long-tailed brownish vole *Caryomys eva*.

Distribution. Left bank of the Minjiang River in southern Gansu, eastern Qinghai, southern Ningxia, north-eastern Sichuan, and western Hubei (Luo et al. 2000, Wang 2003).

Description. Dimensions: BWt=18–27 g, H&B=80–105 mm, TL=44–60 mm, HF=15–20 mm, EL=9–15 mm, CbL=22.0–26.0 mm, ZgW=11.9–14.7 mm, MxT=4.7–6.3 mm. Back is pale brown to dark rusty brown, shaded grey; flanks are tawny ochraceous, underside is greyish slate, washed drab and whitish or buff; feet are white to pale grey. Tail is dark brown above, dull whitish below.

Caryomys eva alcinous (Thomas, 1911)

Microtus (Caryomys) alcinous Thomas, 1911a:4. Type locality: "Wei-chou, Si-ho R[iver], W[estern] Sze-chwan. 8000'–12,000' [2,440–3,660 m]" (Thomas 1912d:140).

Distribution. Right bank of the Minjiang River in central Sichuan in Wenchuan, Baoxing, Kangding, Markam, Heishui, and Zoige (Luo et al. 2000, Wang 2003).

Description. Dimensions: BWt=19–31 g, H&B=82–100 mm, TL=45–60 mm, HF=16–17 mm, EL=10.5–13.2 mm, CbL=21.6–24.0 mm, ZgW=12.3–14.0 mm, MxT=5.2–5.8 mm. Pelage is much darker than in *eva*, and resembles *Eothenomys melanogaster*. Back is dark blackish brown, slightly shaded ochraceous; underside is dark smoky grey (slaty); feet are dark brown. Tail is indistinctly bi-coloured, blackish above and somewhat lighter below.

GENUS: *Eothenomys* Miller, 1900 – Oriental Voles

Eothenomys Miller, 1896:45. Proposed as a subgenus of *Microtus*. Type species: *Arvicola melanogaster* Milne-Edwards.

Taxonomy. *Eothenomys* and *Anteliomys* were established as a subgenera of *Microtus* for voles that occupy topographically rough landscape in south-western China, Taiwan, northern Indochina, north-eastern Myanmar, and Assam (India), and display "a peculiar combination of cranial, dental and external characters" (Hinton 1923:145). In his subsequent work, Hinton (1926a) regarded *Eothenomys, Anteliomys*, and *Caryomys* as a bunch of closely related genera with affinities to *Clethrionomys*, *Craseomys* and *Aschizomys*, rather than to *Microtus*. Later authors frequently included these genera into *Eothenomys*.

In a phylogenetic tree constructed by Liu et al. (2018), *Eothenomys* s.str. was in a sister position against *Anteliomys*+*Eremites* and the major lineages presumably diverged during the Pliocene (~3.51 Mya). Similarly to Hinton (1926a) and Gromov & Polyakov (1977), we classify them as a distinct genera. Alternatively, *Eothenomys* and *Anteliomys* were ranked as congeneric subgenera (Luo et al. 2000) or species groups (*chinensis* and *melanogaster* groups; Musser & Carleton 2005, Lunde 2008).

The number of species recognised in *Eothenomys* s.str. varied over the last century between 1 and 7 and Liu et al. (2018) split the genus into 10 species. In our view, many of the names in Liu et al. (l.c.) are of subspecific value, hence we propose a 3-species arrangement of *Eothenomys*.

Distribution. A broad transitional zone between the Palaearctic and the Oriental realms in Taiwan, China, northern Vietnam, northern Thailand, northern Myanmar and north-eastern India.

Characteristics. Dark and thick-furred voles with greyish brown, dark brown or blackish-brown dorsum and slate-grey belly. Immature individuals are darker while adults are brighter due to rufous hair-tips creating a characteristic bronzy reflection; feet and tail are dusky. Tail is moderately long (normally TL/H&B<0.5); hairs do not conceal the underlying annulation and the terminal pencil is short. The rounded ears overtop the fur; the eyes are small. Whiskers are moderately long, not extending beyond the ears. Feet are small and claws are light, compressed, and of modest length. The thumb on the front feet is relatively heavy and retains a claw. The hind foot has short toes and the plantar surface is hairy from heel to pads. There are 5 palmar and 6 (rarely 5) plantar pads. Metatarsal pads are of approximately the same size as interdigital pads and the rudimentary lateral metatarsal pad (ML in Figure 97) may be entirely absent (Blanford 1881b, Anthony 1941, Tokuda & Kano 1937). Females have 4 inguinal nipples (Allen 1940, Ellerman 1961); Glans penis is barrel-shaped and the terminal crater usually has tiny papillae. The width of the glans amounts to ~50–56% of its length. The baculum is well ossified and of characteristic arvicoline structure, i.e. consisting of a larger proximal baculum with an expanded base and 3 distal bones, of which the medial is the most prominent (for details see Yang et al. 1992, and Liu et al. 2018). Skull is heavy, deep and wide with distinctly bowed zygomata (ZgW/CbL=0.53–0.63). The interorbital region is wide and incisive foramina are short. Larger individuals show a prominent lambdoidal crest and postorbital squamosal process; temporal ridges remain notably apart in the interorbital region. The posterior edge of the palatine is shifted forwards and terminates at the level of the anterior loop of M^3. Auditory bullae have no internal spongy tissue. Upper incisors display a shallow longitudinal groove which is shifted laterally. Molars are rootless and moderately large. M^1 has 4 inner and 3 outer salient angles; M^2 is almost symmetrical with 3 salient angles on each side; M^3 has 3–4 inner salient angles. M_1: dental field T5 is confluent with T6 and the anterior cap; T1–T2 and T3–T4 form transverse prisms (Figure 98). The enamel is either undifferentiated or is thicker on the luff edge; in *E. melanogaster* the enamel band is 0.05 mm thick on either side. The schmelzmuster contains lamellar enamel in the concave (luff) edges of the triangles and tangential enamel in the convex edges (Koenigswald 1980). Karyotype is characterised by a high diploid number (2n=56) of mostly acrocentric chromosomes (Li et al. 2006).

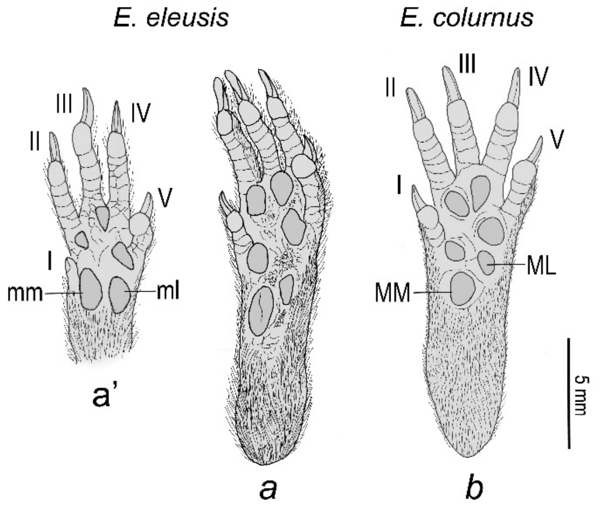


Figure 97: Left palm (a') and sole (a,b) in Oriental voles: a–*Eothenomys eleusis* (O-Quy-Hô, Vietnam). b–*E. colurnus* (Taiwan).

Key to species.

Interspecific differences in Oriental voles are frequently blurred by individual and population variation (cf. Liu et al. 2018) which renders identification by morphological traits vague. The key is therefore to be used with some caution and the identifications made should be checked against more detailed descriptions.

1a) M^3 with 2 re-entrant angles on each side; BR3, if present, is shallow; size small (CbL<25 mm) ………...... 2
1b) M^3 usually with 3 (rarely 2) inner re-entrant angles and 2–3 outer angles; BR3 is usually deep; size larger (usually CbL>25 mm) …………..…..……….............. 4
2a) Dorsal pelage yellowish brown; length of glans penis >4 mm; mean length of proximal baculum=2.6 mm ………………………................. *eleusis shimianensis*
2b) Dorsal pelage reddish brown to blackish brown; length of glans penis <4 mm; mean length of proximal baculum≈2.2 mm ………………………………….. 3
3a) Occurs north of Yangtze………........ *melanogaster*
3b) Occurs south of Yangtze ……………..…. *colurnus*
4a) Bullae longer than MxT....*eleusis* (*eleusis* subspecies group)
4b) Bullae shorter than MxT …………… *eleusis cachinus*

Eothenomys melanogaster (A. Milne Edwards, 1871) – Père David's Oriental Vole

Arvicola melanogaster A. M[ilne] Edw[ards], 1871 (in David 1871:93, footnote pt. 2). Detailed description was subsequently published in Milne Edwards (1872:284, Plates 44 and 44a fig 1). Type locality: "Moupin [Baoxing Xiang] et Sé-Tchouan [Sichuan]."

Taxonomy and nomenclature. Taxonomic scope follows Liu et al. (2018) and Tang et al. (2018). In the past, *melanogaster* was understood in a much broader sense (e.g. Luo et al. 2000, Kaneko 2002, Lin et al. 2020), and at one point was the only recognised species of

Eothenomys (Ellerman & Morrison-Scott 1951). Even in a narrower view, *colurnus* was usually included as a subspecies of *melanogaster* (Howell 1929, Wang 2003).

The correct year of publication is disputed. Volume 7 of the *Bulletin des Nouvelle archives du Muséum* has 1871 on the front page, which was followed by earlier authors (Trouessart 1897:552, Palmer 1904:84, Allen 1940:806, Rode 1945:101). The year 1872 is first mentioned in the *Zoological Record for 1872* (Günther 1874:13) and again in Ellerman & Morrison-Scott (1951:668). Ellerman & Morrison-Scott quote other names from the same volume of the *Bulletin* (e.g. *Ailurops* Milne Edwards on p. 242) as being published in 1871.

Distribution (Figure 99). Mountains encircling the Sichuan Basin in southern China to the north of the Yangtze and Dadu Rivers. The range covers an estimated 135,560 km² in western Hubei, northern Chongqing, southern Shaanxi, southern Gansu, and central Sichuan; there is an isolate in southern Ningxia. Occupies agricultural land, meadows, rhododendron thickets and forests (broadleaf evergreen and deciduous, coniferous) at altitudes of 500–3,400 m (Allen 1940, Luo et al. 2000, Tu et al. 2012, Sun et al. 2013); not sympatric with another *Eothenomys* anywhere.

Characteristics. Size is medium for *Eothenomys*: BWt=19–29 g, H&B=85–112 mm, TL=29–45 mm, HF=15–18 mm, EL=8–13 mm, CbL=21.7–26.0 mm, ZgW=12.2–16.2 mm, MxT=5.0–6.7 mm. Tail is of average length (TL/H&B=0.31–0.48) and moderately hairy; the underlying annulation is visible and the pencil is short. Ears are sparsely covered with hair. Fur is sleek and glossy, uniformly clear brown to blackish brown above, ashy grey to dark slaty below (cf. Plate 44 in Milne Edwards 1872). Feet are dusky brown; the tail is blackish brown above, slightly paler below. The glans penis (length=3.6–4.4 mm, width=2.4–2.5 mm) is cylindrical and wide; its apex is truncate and the urethral lappet in the pennial crater has 3 terminal forks (Yang et al. 1992). Dimensions ($\bar{x}$±SD; mm) of proximal baculum in adult voles: length=2.12±0.21; length of medial and lateral distal bones=1.07±0.14 and 0.80±0.15, respectively (Liu et al. 2018). The skull is rather deep and zygomatic arches are distinctly bowed (ZgW/CbL=0.56–0.62). Rostrum is broad, bullae are moderately large and the interorbital region is wide (Figure 100). In comparison to *eleusis,* the M^3 is less complex, usually with 2 deep lingual re-entrant angles; the postero-lingual angle LR4 is either shallow or absent (Figure 98a).

Variation and subspecies. Monotypic species.

Eothenomys colurnus (Thomas, 1911) – Fujian Oriental Vole

Distribution (Figure 101). South-eastern China (south of the Yangtze River) in south-eastern Anhui, Zheijang, Fujian, and eastern Jiangxi, with 3 isolates: (i) northern Guangdong, (ii) western Jiangxi and (iii) Taiwan. Range covers an area of 83,945 km² and the altitudinal range is 200–3,200 m.

Characteristics. Similar to *E. melanogaster*; tail is moderately long (TL/H&B=0.29–0.49), hairy with a short pencil (2.5–3.0 mm). Fur is short and velvety, dull rich reddish-brown to blackish brown above, ashy grey to dull-slate below; transition is rather definite in brown animals and obscured in blackish ones. Occasionally there is a buffy spot on the hip. Tail is blackish-brown to black, either slightly lighter below or dark throughout; ears are grey to blackish. The urethral lappet in the penial crater has 3 terminal forks. Dimensions ($\bar{x}$±SD; mm) of glans penis are length=3.60±0.18 and width=1.88±0.10; proximal baculum in the nominal subspecies is 2.28±0.10 long and 1.28±0.15 wide at the basal expansion; length of medial and lateral distal bacula is 1.13±0.10 and 0.84±0.05, respectively (Liu et al. 2018). Skull and dentition show no peculiarities (Figure 100). Zygomatic arches are expanded (ZgW/CbL=0.57–0.62); incisive foramina are short and wide with bowed lateral margins. Squamosal protuberance is prominent and the skull tends to be deeper than in *melanogaster*. Molars as in *melanogaster* (Figure 98b); M^3 has 3 labial salient angles in 94.4% of individuals (Kaneko 2002). Karyotype is known only for *E. c. kanoi*: 2n=56, NF_a=56; all chromosomes are acrocentric except 1 pair of small metacentric autosomes (Harada et al. 1991; Li et al. 2006).

Variation and subspecies. The insular and mainland populations are usually regarded as subspecifically distinct (e.g. Luo et al. 2000).

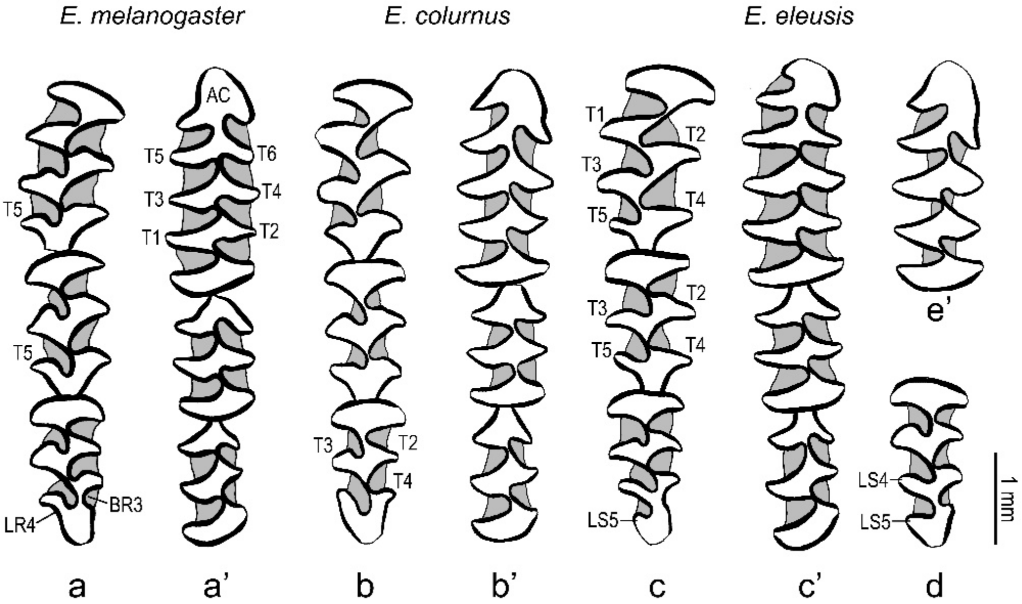


Figure 98: Molar pattern in Oriental voles. *Eothenomys melanogaster*: upper (a) and lower row (a'–Washan, Sichuan, China). *E. colurnus*: upper (b) and lower row (b'–Fukien, Kuantun, China). *E. eleusis*: upper (c) and lower row (c'–Quy-Hô, Vietnam); isolated M^3 (d–Yangpi, Yunnan, China) and M_1 (e'–Lijiang, northern Yunnan, China).

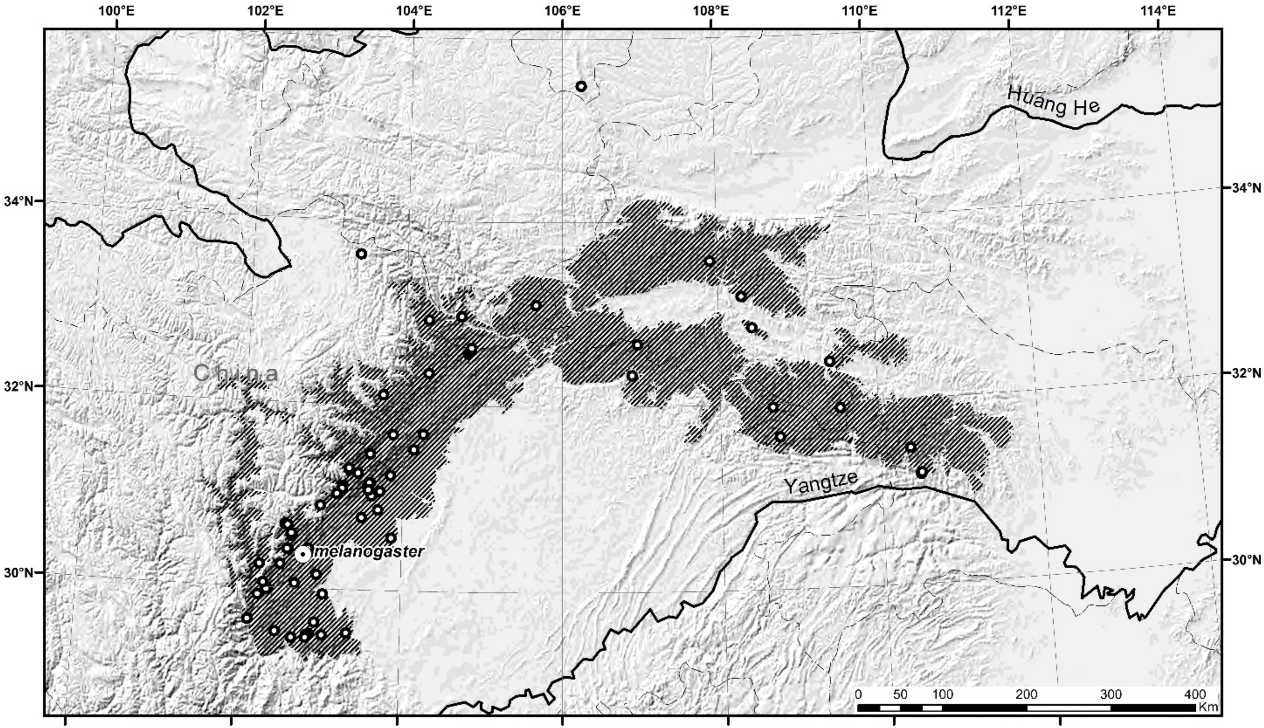


Figure 99: Distributional range of Père David's Oriental vole *Eothenomys melanogaster*.

Eothenomys colurnus colurnus (Thomas, 1911)

Microtus (Eothenomys) melanogaster colurnus Thomas, 1911.g:209. Type locality: "Kuatun, N.W. Fokien [= Fujian]", China.

Synonyms. *Microtus bonzo* Cabrera, 1922.

Distribution. The mainland part of the species' range. Mountains (mainly>1000m); abundance positively correlates with altitude (Bao & Zhuge 1986).

Characteristics. On average larger and lighter than *kanoi*. Back uniformly rich brown and shaded rusty, belly is slate-silver, demarcation is distinct. Dimensions: H&B=96–137 mm, TL=24–41 mm, HF=16–17 mm, EL=10–16 mm, CbL=23.2–26.4 mm, ZgW=14.0–15.7 mm, MxT=5.4–7.0 mm.

Eothenomys colurnus kanoi Tokuda, 1937

Eothenomys kanoi Tokuda, 1937 (in Tokuda & Kano 1937:1118 (captions to Figs. 2, 3 & 4). Type locality: "Sikayau Hsau, 5500 – 7500 feet [1,675–2,285 m]", Taiwan.

Distribution. Endemic to Taiwan where they are restricted to bamboo grasslands, broad-leaf and mixed

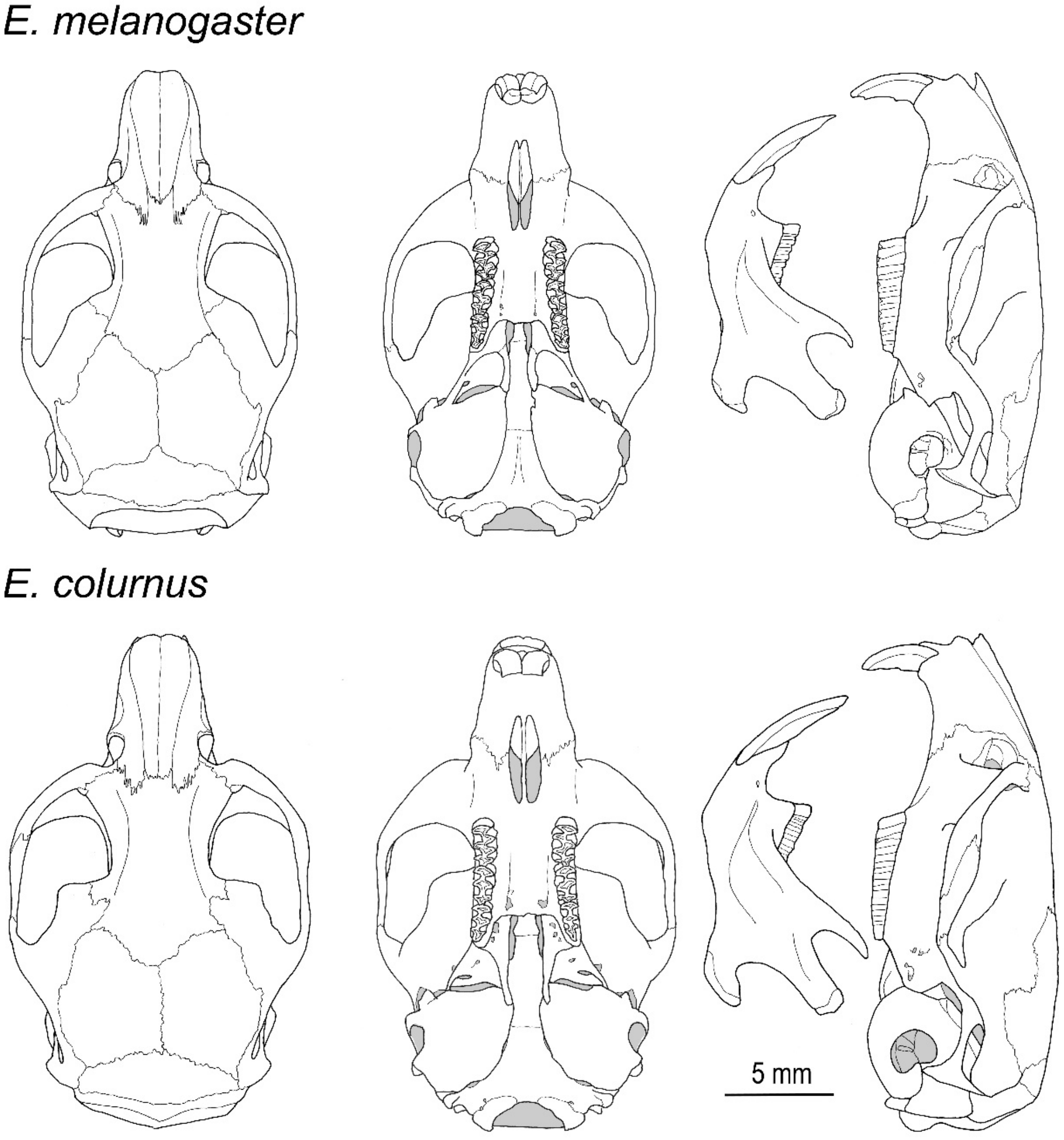


Figure 100: Skull and mandible in Oriental voles: top–*Eothenomys melanogaster* (Washan, Sichuan, China); bottom–*E. colurnus* (Taiwan).

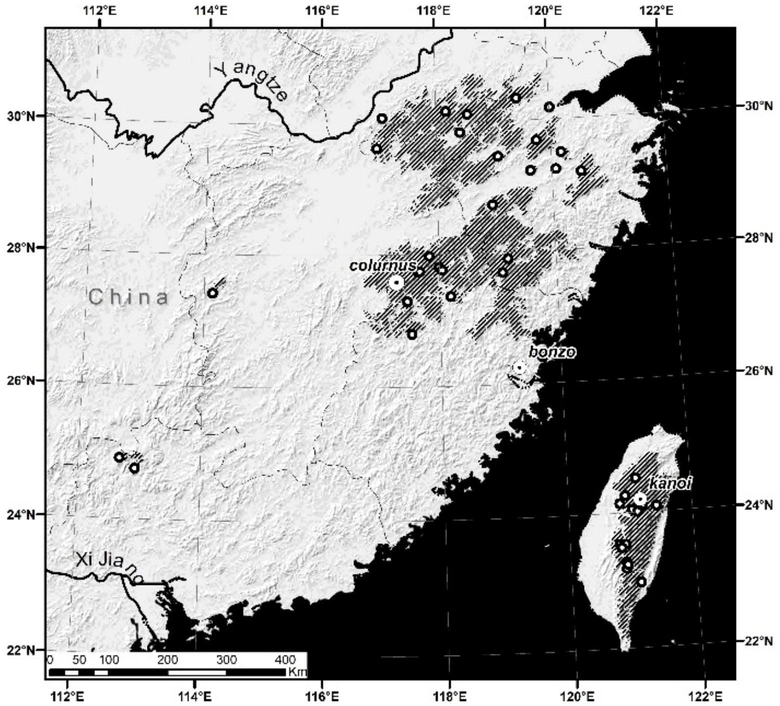


Figure 101: Distributional range of the Fujian Oriental vole *Eothenomys colurnus*.

forests at 1,400–2,680 m (Yu 1994). The island was likely repeatedly colonised from the mainland during cold phases in the Pleistocene when the Taiwan Strait acted as an intermittent land bridge (Lv et al. 2018).,

Characteristics. On average smaller and darker than the nominotypical subspecies. Dimensions: BWt=14.6–28 g, H&B=82–110 mm, TL=30–43 mm, HF=14.2–16.7 mm, EL=8.1–11.7 mm, CbL=22.8–25.0 mm, ZgW=13.2–15.0 mm, MxT=5.8–6.5 mm. Back is dull brown to blackish brown; belly is slate-grey to slate-black, interspersed with silver hairs in some voles and washed brown in others. Feet blackish but tips of the toes white in some individuals; claws are amber. There are 5–6 plantar pads; the lateral metatarsal pad is absent (Tokuda 1941).

Eothenomys eleusis (Thomas, 1911) – Yunnan Oriental Vole

Taxonomy. Taxonomic scope of *eleusis* changed over time and is still far from settled. All imaginable combinations of taxonomic names have previously been proposed (cf. Table 1 in Liu et al. 2012a). Most commonly, *eleusis* was synonymised with *melanogaster* or regarded as a species in its own right, either as a monotypical taxon (Jiang et al. 2015), in combinations with *confinii* (Allen 1940), or with *aurora* and *yingjianensis* (Luo et al. 2000, Wang 2003). *E. miletus, fidelis* and *cachinus* were occasionally classified as distinct from *eleusis* (Allen 1940, Luo et al. 2000, Liu et al. 2018, 2020a). Liu et al. (2018) proposed the most split taxonomy with 5 species. Pairwise genetic divergences between three of their species (*eleusis*, *fidelis* and *miletus*) are inside the overlapping "grey zone" between the inter- and intraspecies heterogeneities (K2P=3.9–4.1%) and we rank them as conspecific. Two further taxa (*cachinus* and the newly described *shimianensis*) are more diverged (K2P=5.3–6.3%; Liu et al. 2018), however the haplotypes of *eleusis* and *cachinus* are sympatric over an extensive area (Lv et al. 2018). And finally, various sublineages of *cachinus* (*cachinus s. str.*, *libonotus* and *confinii*) do not form monophyletic lineages (Liu et al. 2018). We therefore treat all these taxa as conspecific.

The taxonomic relationships of a further 2 names are uncertain. In the past *mucronatus* was as a rule synonymised with *melanogaster*. Kaneko (2002) extracted *mucronatus* from *melanogaster* and used it in his 2-species classification of *Eothenomys* as the oldest name for the larger species with a complex M^3. The genetic identity of *mucronatus* is not known, however the area around the type locality is occupied by *eleusis* which caused us to synonymise *mucronatus* with *eleusis*. Vouchers in the type

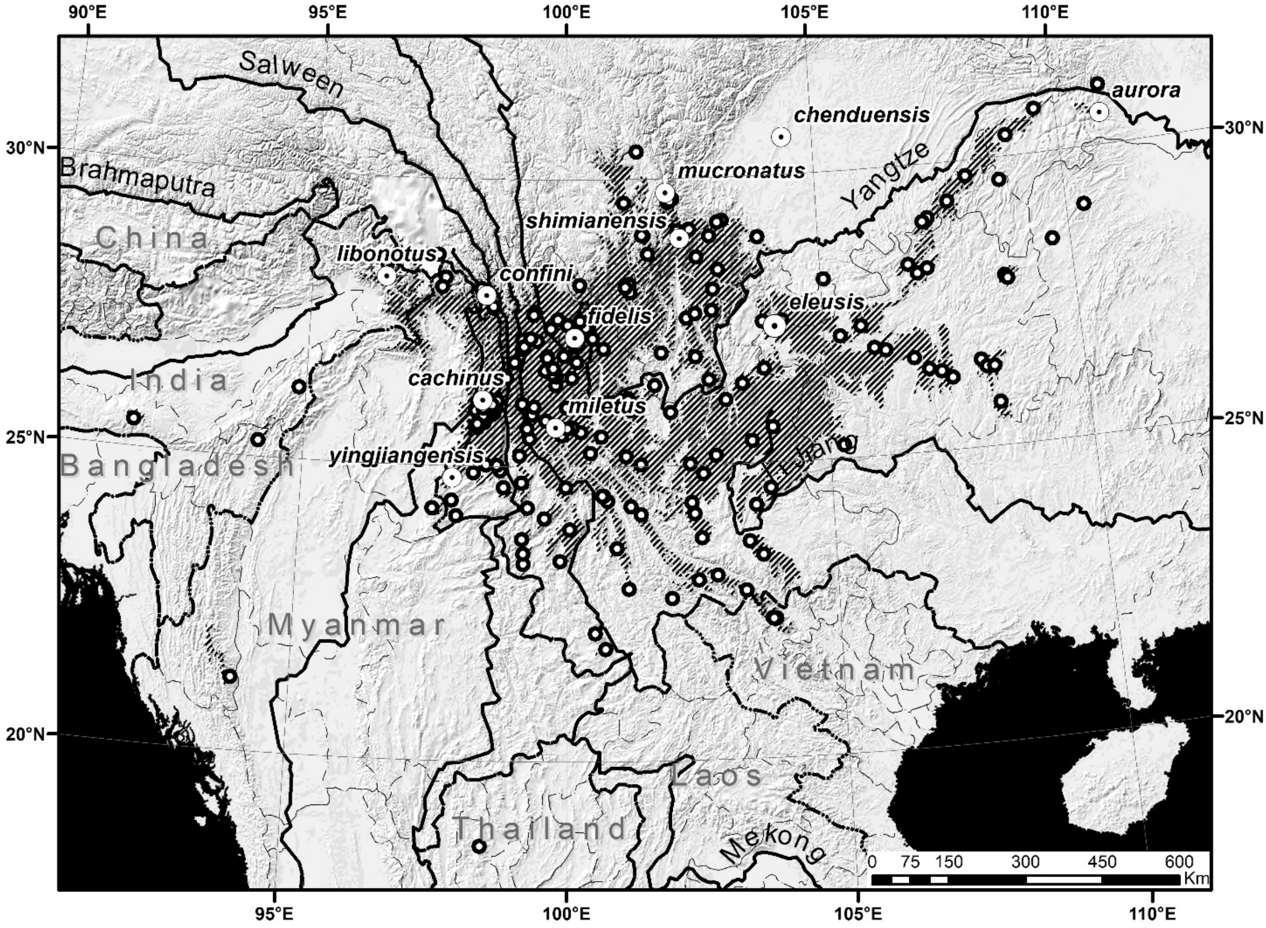


Figure 102: Distributional range of the Yunnan Oriental vole *Eothenomys eleusis*.

series of *mucronatus* are larger than *melanogaster* but M^3 has 3 salient angles on each side with "indications of a small additional pair of angles, one on the outer and one on the inner side of the posterior heel" (Allen 1912: 215). The next name is *chenduensis,* which is generally regarded as conspecific with *melanogaster*. Wang & Li (in Luo et al. 2000) based *chenduensis* on its light colouration (brown or buff brown vs dark and dull in *melanogaster* s. str.) and much bigger size (BWt=29–46.5 g and skull length=27.8–28.2 mm in *chenduensis* vs 19–29 g and 22.5–25.1 mm, respectively, in *melanogaster* s. str.). In size and colour *chenduensis* therefore matches *eleusis*.

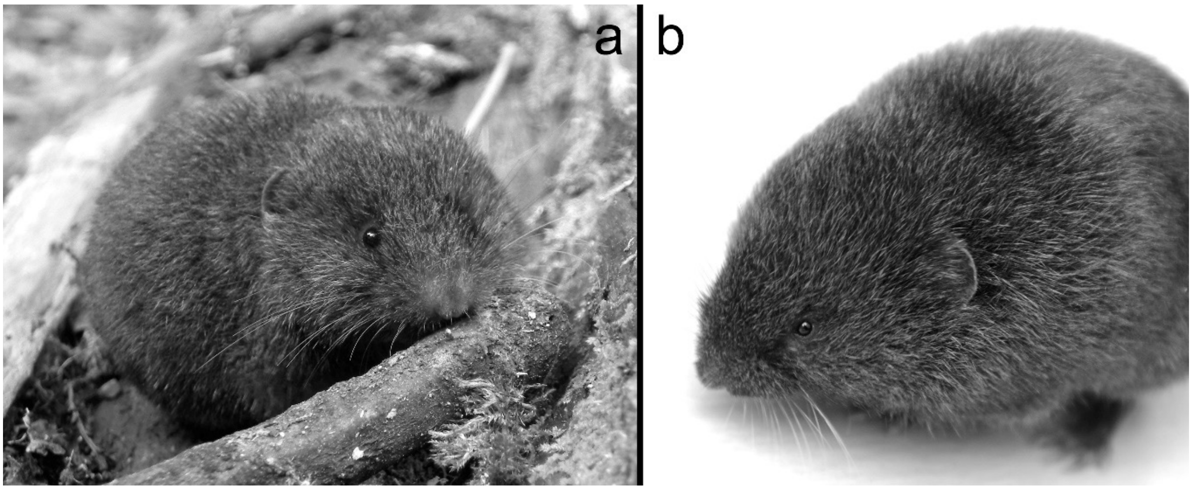
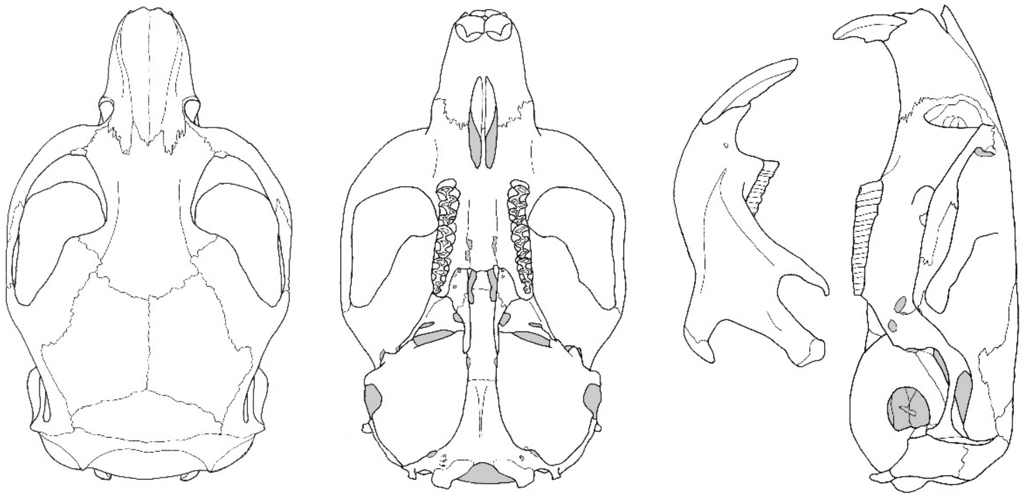


Figure 103: Yunnan Oriental voles *Eothenomys eleusis* from (a) Mt. Jinfo, Nanchuan District, Chongqing (~1,800m a.s.l.), and (b) Mt. Tanhua, Dayao county, Chuxiong Prefecture, Yunnan (~1,300m a.s.l.); both China. Photo courtesy Kai He & Tao Wan (a) and Kai He (b).

Distribution (Figure 102). South-western mountains encircling the Sichuan Basin and Gaoligong Mts.; in the west the range encompasses Myanmar and the Mishmi Hills in Arunachal Pradesh (India), in the south it reaches mountains in northern Vietnam (in Lào Cai) and northern Thailand; to the north-east the range transgresses the Yangtze Valley in Yichiang (Hubei; Liu et al. 2018). The vast majority of the range is in China in western Hubei, western Hunan, southern Shanxi, southern Gansu, Sichuan, Chonguing, Guizhou, Yunnan, and south-eastern Xizang (Tibet). The area is estimated at 318,090 km^2. A wide range of habitats is occupied from farmland and grassy meadows, to scrub-covered hillsides, bamboo thickets, and various types of woodland (humid evergreen broadleaf forests, dark coniferous forests) with light and humid soil; absent from dry lowland forest plantations. Altitudinal range is 650–4,250 m (Hinton 1923). The southernmost records are from altitudes of 1,320 m (Vietnam) and 2,575 m (Thailand; Kaneko 2002).

Characteristics. Size is medium to large, tail is relatively long (TL/H&B=0.35–0.56); the eyes are small (Figure 103) and the ears are short and rounded, thinly covered with minute hair. Lateral metatarsal pad is distinctly smaller than the medial and subdigital pads (Figure 97a). Fur is long for Oriental voles (up to 11 mm). Colour is variable: upper parts are reddish brown with bright-

E. eleusis eleusis



E. eleusis cachinus

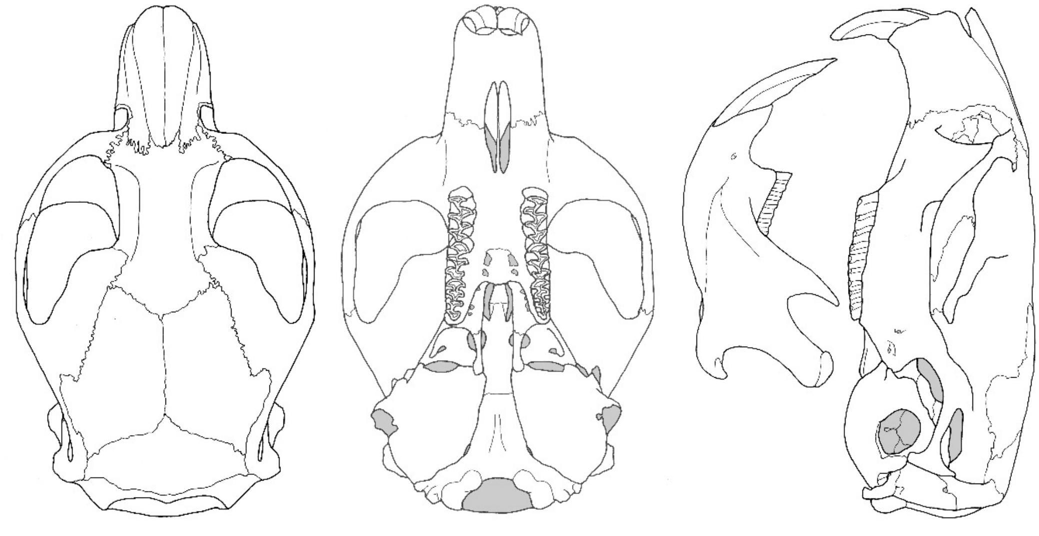


Figure 104: Skull and mandible in *Eothenomys eleusis*: top–ssp. *eleusis* (Chao-tung-fu, northern Yunnan, China); bottom–ssp. *cahinus* (Kachin, Myanmar).

yellow brassy reflections, dark brown shaded bright rufous or greyish brown; the snout is occasionally grizzled grey. The underside is grey to slate grey, sometimes with a hoary appearance. Feet are dusky or brown with greyish reflections; tail is indistinctly bicoloured, blackish above, greyish below.

Skull is large and heavy with prominent temporal ridges and post-orbital squamosal crests; auditory bullae are moderately large to large (Figure 104). The zygomata are stouter and bowed (ZgW/CbL=0.53–0.63). Posterior palatal foramina are large, the edge of the palate is complete and simple, not forming a spinous process. Incisive foramina short and wide; the mandible is heavy. Molars show no marked peculiarities; M^3 has 4 salient angles on lingual side in ~90% of individuals. M_1 has 4–5 inner, and 3–4 outer re-entrant angles; consequently, there are 2–3 transverse loops, each formed by widely confluent dental fields of alternating triangles (Figure 98c,d).

All chromosomes ($2n=56$, $NF_a=54$) are acrocentric (Wu et al. 1989, Chen et al. 1994, Li et al. 2006).

Variation and subspecies. We define *eleusis* as a polytypic species with 5 highly divergent subspecies which cluster in 3 subspecies groups (*eleusis, cachinus* and *shimianensis* groups).

The major discrepancy between sources is not in recognising lineages as distinct taxa but in ranking them as species (e.g. Liu et al. 2018) or subspecies (this review).

Subspecies group *eleusis*

Eothenomys eleusis eleusis (Thomas, 1911)

Microtus (Eothenomys) melanogaster eleusis Thomas, 1911b:50. Detailed description followed in Thomas (1912d:139). Type locality: "21 miles [34 km] east of Chao-tung-fu, N.[orthern] Yunnan. 5800' [1,770 m]" (Thomas 1912d:139), China.

Synonyms. *Microtus aurora* G. M. Allen, 1912. *Eothenomys melanogaster chenduensis* Wang & Li, 2000.

Distribution. The eastern part of the species' range to the south of the Yangtze River (with a single isolate to its north in Chengdu, eastern Sichuan) and between the Red River – western Hubei – eastern Yunnan; also northern Vietnam and northern Thailand.

Description. The smallest subspecies in the group: BWt=21–30 g, H&B=90–105 mm, TL=33–55 mm, HF=14–18.5 mm, EL=9–13.5 mm, CbL=23.1–25.1 mm, ZgW=12.9–15.1 mm, MxT=5.1–6.6 mm. The tail is longer (TL/H&B≈0.45) than in *miletus* and *fidelis* (≈0.4). Colour varies from reddish brown with bright-yellow brassy reflections to greyish brown. Glans penis is short ($\bar{x}$±SD=3.96±0.16 mm) and narrow (2.00±0.11 mm); the urethral lappet with 3 forks. Baculum of moderate size, length of proximal bone=2.59 ±0.11 mm, of distal baculum=1.33±0.15 mm (Liu et al. 2018). M^3 usually with 4 inner and 3–4 outer salient angles.

Eothenomys eleusis miletus (Thomas, 1914)

Microtus (Eothenomys) miletus Thomas, 1914a:474. Type locality: "10 miles [16 km] W.[est] of Yang-pi [Yangpi], W.[estern] Yunnan", China.

Distribution. Range is in 2 fragments. The larger segment is in the mountains between the Dadu and Yalong Rivers in southern Sichuan and in the south-western edge of the Sichuan Basin. The smaller segment is between the Mekong and Red Rivers in Yunnan (Liu et al. 2018).

Characteristics. Body massive, size large: BWt=29–47 g, H&B=100–126 mm, TL=39–53 mm, HF=17–21 mm, EL=11–16 mm, CbL=25.0–28.7 mm, ZgW=14.0–17.2 mm, MxT=5.8–7.2 mm. Tail is shorter than in ssp. *eleusis*. Back is dull greyish brown, occasionally shaded buff; ventral side is grey and transition is undetectable to distinct. Glans penis is short ($\bar{x}$±SD=3.96±0.20 mm) and rather narrowed (2.19±0.12 mm); the urethral lappet with 3–4 forks. Baculum of moderate size, length of proximal bone=2.52 ±0.09 mm, distal baculum=1.25±0.10 mm (Liu et al. 2018). M^3 with 3–4 salient angles on each side.

Eothenomys eleusis fidelis Hinton, 1923

Eothenomys fidelis Hinton, 1923:150. Type locality: "the [north-western] flank of the Lichiang [Lijiang] Range in latitude 27° 30' N[orth] … Altitude 14,000'[4,270 m]", northern Yunnan, China.

Synonyms. *Microtus mucronatus* G. M. Allen, 1912.

Distribution. Mountains between the Yalong and Red Rivers in southern Sichuan and adjacent Yunnan.

Characteristics. Size large: BWt=25–43 g, H&B=100–120 mm, TL=36–49 mm, HF=16–22 mm, EL=10–16 mm, CbL=24.7–28.6 mm, ZgW=14.3–16.6 mm, MxT=5.7–7.2 mm. Voles are smaller in Yunnan. Tail is relatively short. Upper parts are dark brown shaded bright rufous, underside slate grey with a hoary tinge. Feet and tail are dusky. Glans penis long ($\bar{x}$±SD=4.43±0.24 mm) and wide (2.35±0.22 mm); the urethral lappet with 2 (rarely 3) forks. Baculum large, length of proximal bone=2.73±0.24 mm, distal baculum=1.41±0.18 mm (Liu et al. 2018). M^3 usually with 4 inner and 3–4 outer salient angles.

Subspecies group *cachinus*

Eothenomys eleusis cachinus (Thomas, 1921)

Microtus (Eothenomys) cachinus Thomas, 1921:504. Type locality: "Imaw Bum, 9,000' [2,745 m]", Kachin State, Myanmar.

Synonyms. *Eothenomys melanurus confinii* Hinton, 1923; *Eothenomys melanurus libonotus* Hinton, 1923; *Eothenomys eleusis yingjiangensis* Wang & Li, 2000.

Taxonomy. In the past *cachinus* was usually synonymised with *melanogaster* or rarely with *mucronatus* (e.g. Kaneko 2002). More recently, *cachinus* began to be regarded as a species in its own right, although its taxonomic scope was narrower than proposed here (Luo et al. 2000; Wang 2003). Its junior synonyms, as specified above, were linked with various names: *confinii* with *eleusis* (Allen 1940), *miletus* (Luo et al. 2000; Wang 2003) or *mucronatus* (Kaneko 2002), *libonotus* with *melanogaster* (Agrawal 2000; Ellerman 1961; Wang 2003) or *mucronatus* (Kaneko 2002), and *yingjiangensis* with *melanogaster* (Kaneko 2002) or *eleusis* (Wang 2003). In synonymising *libonotus* and *confinii* with *cachinus* we follow Liu et al. (2018).

The Kachin Oriental vole displays considerable individual and interpopulational variability. Two allopatric races were distinguished in the past: (i) a mountain form (2,300–3,200 m a.s.l.) with a longer tail (TL/H&B=0.44) and a complex M^3 (usually classified as *cachinus* and also including *confinii*), and (ii) an intermediate foothills form (1,550–2,750 m) with a shorter tail (TL/H&B=0.36) and a simple M^3 (*libonotus*). They were either classified as conspecific (Anthony 1941) or as distinct species (Luo et al. 2000; Musser & Carleton 2005).

Distribution. Gaoligong Mts. in north-western Yunnan, south-eastern Xizang (Tibet), Myanmar, and the Mishmi Hills in Arunachal Pradesh (India). The identity of Oriental voles from scattered localities in Chin Province (Myanmar), the Naga Hills (Nagaland), Manipur Hills in Manipur (Kaneko 2002) and Khasi Hills in Meghalaya is not known with certainty and we tentatively treat them as *cachinus*. The subspecies occupies grassy meadows, shrubs and various types of woodland at 1,550–3,700 m a.s.l. (Anthony 1941, Cranbrook 1961, Kaneko 2002).

Characteristics. Size is modest: BWt=18–42 g, H&B=85–117 mm, TL=28–43 mm, HF=15–18.5 mm, EL=10–14 mm, CbL=22.2–27.2 mm, ZgW=13.1–16.1 mm, MxT=5.1–7.4 mm. Relative length of tail is moderate to long (TL/H&B=0.31–0.57). Fur is dense and soft; tail is sparsely hairy with a short terminal pencil. There are 5–6 plantar pads (Anthony 1941). Upper parts are dark and rich brown, brightened by dull golden or rufous hair-tips. Flanks are faintly lightened and the belly is slaty-grey; the transition is obscured. Tail is blackish throughout and only indistinctly lighter beneath; feet are a similar colour but slightly lighter. Glans penis is long ($\bar{x}$±SD=4.39±0.26 mm) and rather narrow (2.33±0.16 mm); the urethral lappet with 3 (rarely 4) forks. Baculum is long; length of proximal bone=2.75 ±0.15 mm and distal baculum=1.31±0.06 mm (Liu et al. 2018).

Skull is heavy and deep with distinct though weak temporal ridges. In comparison with *eleusis* and *shimianensis,* the dorsal contour is flatter in the interorbital region. Zygomatic arches expand widely (ZgW/CbL=0.58–0.61); the interorbital region is long and parallel-sided; bullae are distinctly small. Cheek-teeth are large; M^3 has 3–4 inner and outer salient angles; 3 inner angles are seen in about 15% of individuals and 3 outer angles in half of all animals (Liu et al. 2018).

Subspecies group *shimianensis*

Eothenomys eleusis shimianensis Liu, 2018

Eothenomys shimianensis Liu, 2018 (in Liu et al. 2018:26, Figs 6A & 9C). Type locality: "Liziping National Nature Reserve, Shimian County, Yaan, southwestern Sichuan (28.93888^{0}N, 102.24837^{0}E; elevation 2390 m)", China.

Taxonomy. *E. shimianensis* holds a sister position against *E. cachinus* in the phylogenetic tree (Liu et al. 2018).

Liu et al. (2018) quote Shaoying (also spelled Shao-ying) as the author of the taxonomic name. Full name of the author is Shaoying (forename) Liu (surname). The Code stipulates that the fore- and surname "be distinguished as in scientific bibliographies" (Recommendation 51B).

Distribution. Known only from Shimian County, Sichuan, China, where present at altitudes 1,850–2,600 m. Habitat is moist broadleaf forest with dense grass and bamboo understory on light sandy soil with deep humus layer; also found in dense grassland (Liu et al. 2018).

Characteristics. Size moderate: H&B=92–109 mm, TL=37–45 mm, HF=16–19 mm, EL=10–13 mm, CbL=23.4–25.2 mm, ZgW=13.4–14.7 mm, MxT=5.5–6.1 mm (Liu et al. 2018). Tail is relatively long (TL/H&B=0.38–0.46); hair is rather short (~7.5 mm), ears are hairy and overtop the fur. Vibrissae (length up to 25 mm) are dark grey, some white tipped. Dorsal pelage is yellow-brown, the snout and ocular region are slate, interspersed with yellow hairs; ventrum is slate-grey, transition on the flanks is gradual. Tail is grey-black above, grey-white below; paws are grey-black. Glans penis is 4.3 mm long and 2.2 mm wide; urethral lappets with 3 forks, each fork further split into 2 finger-like processes. Dimensions of proximal baculum: length=2.6 mm, width of basal expansion=1.5 mm; length of medial and lateral distal bacula is 1.3 mm and 1.1 mm, respectively (Liu et al. 2018). The skull is relatively narrow (ZgW/CbL=0.57–0.59) and rather deep. The orbital region is wide, interparietal is large, squamosal crest is prominent and bullae are small (Figure 104). Incisive foramina are short and wide. M^3 has 3 lingual and 2 labial re-entrant angles; the posterior inner salient angle LS5 is feeble. M_1 with 4 inner and 3 outer re-entrant angles; the antero-buccal angle BS4 is poorly developed. The inner and outer salient loops of M^3 are nearly symmetrical.

GENUS: *Anteliomys* Miller, 1896 – Chinese Voles

Taxonomy. Genetic divergence between *Eothenomys* and *Anteliomys* exceeds the divergences separating *Alticola, Clethrionomys* and *Craseomys* (Kohli et al. 2014) hence we treat *Anteliomys* as a genus in its own right.

Distribution. The genus occupies the Palaearctic-Oriental transition, and is known from the Hangduan Mts. in south-western China (south-western Sichuan and northern Yunnan) and marginally in Myanmar. Many species were long "known only from the type locality" (Osgood 1932: 322) and their ranges are genuinely small (<45,000 km^2).

Characteristics. External morphology much as in *Eothenomys*. Back is brown and belly is grey; hair frequently has light tips, giving "frosty" appearance. There are 5 palmar and 6 plantar pads; the lateral metatarsal pad is the smallest. Females have 4 inguinal nipples. Temporal ridges converge in the interorbital region but never fuse into the sagittal crest; the posterior palate frequently has a blunt medial spinous process. Auditory bullae are without internal spongy tissue. The postero-lingual salient angle LS4 is absent on M^1–M^2; buccal re-entrant angle BR2 is the deepest outer syncline in many species. The antero-labial triangle T2 is frequently confluent with the anterior lobe on M^3 ("*Alticola*" morphotype); the enamel pattern is complex with 4–5 salient angles on the inner side and occasionally elongated posterior cap. The enamel is thicker on the luff edge (positive differentiation). The karyotype (2n=32; known only in *proditor*) is profoundly different from that of *Eothenomys* (2n=56).

Key to species

1a) M^3 with shallow antero-buccal re-entrant angle BR1; dental field of T2 is widely confluent with the anterior lobe ……………………………………………… 2
1b) M^3 with deep antero-buccal re-entrant angle BR1, isolating dental field of T2 from the anterior lobe; TL/H&B>0.5 ……………………………… *tarquinius*
2a) Size large: BWt≥38 g, HF>20 mm, EL>15 mm; tail long: TL/H&B>0.5; distal baculum longer than ½ the proximal baculum ………………………………… *chinensis*
2b) Size smaller: BWt ≤39 g, HF≤20 mm, EL≤15 mm; tail usually shorter: TL/H&B<0.5; distal baculum shorter than ½ the proximal baculum ……………… 3
3a) M^2 with posterior lingual salient angle LS4 present (3 inner salient angles) (occasionally missing in *custos*) ……………………………………………………… 4
3b) M^2 with posterior lingual salient angle LS4 absent (2 inner salient angles) ……………………………………… 5
4a) Smaller: BWt<20 g; tail shorter (<30 mm), TL/H&B≈0.25; M^2 with posterior lingual salient angle LS4 prominent (of about the same size as LS3) …………………………………………………… *olitor*
4b) Larger: BWt>20 g; tail longer (>30 mm); TL/H&B≈0.35–0.5; M^2:posterior lingual salient angle LS4 blunt, much smaller than LS3 ……………… *custos*
5a) M^3 with 5–6 inner salient angles; angular process sickle-shaped (long and slim); bullae of same length as MxT ……………………………………………………… 6
5b) M^3 with 3–4 inner salient angles; angular process short and blunt; bullae shorter than MxT………. *proditor*
6a) Dorsal pelage blackish grey; urethral lappet on glans penis with 4–6 forks; proximal baculum short (length<3.7 mm); dental fields T2–T3 on M^2 usually confluent ………………………………………………… *wardi*
6b) Dorsal pelage greyish-brown; urethral lappet on glans penis with 2–4 forks; proximal baculum long (length>3.8 mm); dental fields T2–T3 on M^2 isolated ……………………………………………………… *hintoni*

SUBGENUS: *Anteliomys* Miller, 1896

Anteliomys Miller, 1896:47. Type species: M*icrotus chinensis* Thomas. Proposed as a subgenus of *Microtus*.

Taxonomy. Subgenus *Anteliomys* further splits into 2 species groups (*chinensis* and *wardi* groups) which are geographically segregated. The *chinensis* group occupies the eastern part, and *wardi* group occupies the north-western segment of the subgeneric range. The taxonomic scope of the *chinensis* species group as is defined here is narrower than in Musser & Carleton (2005) and Lunde (2008).

Species group *chinensis*

Anteliomys chinensis (Thomas, 1891) – Long-tailed Chinese Vole

Microtus chinensis Thomas, 1891a:117. The type was reportedly "taken […] in West Sze-chuen at the same time [as] *Hipposiderus Prattis*" but no further details accompany the description. The type locality of *Hipposideros prattis* is "Kia-ting-fu [Leshan], Western Sze-chuen [Sichuan], China" (Thomas 1891b:527).

Taxonomy. Until recently, *chinensis* included *tarquinius* and in some opinions also *wardi*. Present taxonomic scope follows Liu et al. (2012a).

Distribution (Figure 105). Mountains in southern Sichuan along lower reaches of the Dadu and Minjiang Rivers, in Qingshen, Emeishan, Leshan, Hanyuan and Meigu. The species is known from 6 localities and its distribution area (1,580 km²) is the smallest in the genus. *A. chinensis* lives in broadleaf and coniferous forests, mountain bushes and meadows at altitudes 430–3,400 m (Kaneko 1996b).

Characteristics. A large and long-tailed (TL/H&B=0.55–0.85) vole with prominent ears. Dimensions: BWt=38–57 g, H&B=102–134 mm, TL=57–71 mm, HF=21–25 mm, EL=16–20 mm,

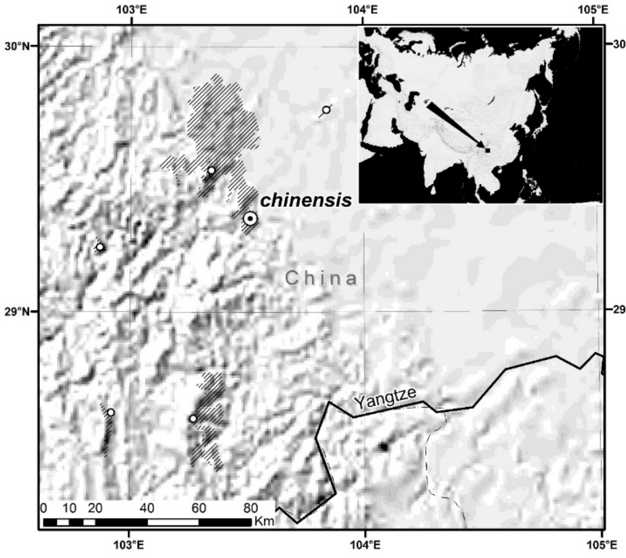


Figure 105: Distributional range of the long-tailed Chinese vole *Anteliomys chinensis*.

CbL=26.6–30.7 mm, ZgW=16.4–18.4 mm, MxT=6.4–7.1 mm (Zeng et al. 2013). Tail is thinly haired; the sole is hairy between the heel and the pads which are prominent; the thumb has a distinct nail. Fur is very long (up to 12 mm in midback), dark brown with a rusty tinge on dorsum, slate grey with brown tints below; the tail is indistinctly bi-coloured, dark brown above, slightly paler below; feet are dusky. The urethral crater on the glans penis is funnel-shaped and widely expanded; distal baculum (length=1.30–1.58 mm) is proportionally long, comprising on average 56% of the length of the proximal baculum (length=2.40–2.83 mm; Zeng et al. 2013). Skull is robust and angular with prominent parietal crests. Incisive foramina are moderately large and broadly oval (Figure 106). M^3 is long and complex with 5 (rarely 4) lingual and 4 buccal salient angles; the posterior lingual triangles have no counterparts on the outer side except for a faintly noticeable shallow salient angle BS5. M_1 is rather simple with 5 inner and 4 outer salient angles; dental fields of T6 are widely confluent with the anterior cup (Figure 107a,a’).

Variation and subspecies. Monotypic species.

Anteliomys olitor (Thomas, 1911) – Dwarf Chinese Vole

Taxonomy. Hinton (1926a) excluded *olitor* (along with *proditor*) from *Anteliomys*, placing them into *Eothenomys* s.str. In the past both species were occasionally classified in *Caryomys* (Pavlinov et al. 1995). Molecular reconstructions retrieved *olitor* and *proditor* as sister species of *Anteliomys*. Zeng et al. (2013) regarded them as the least differentiated species tandem of the genus which contradicts the subsequent estimation of divergence time at 1.40 Mya (Liu et al. 2018).

Distribution (Figure 108). The southernmost part of the range of *Anteliomys*, south of 27°40’ northern latitude. Records are comparatively few and are widely scattered in the mountains of northern Yunnan between the Yangtze, Xi Jiang, and Salween Rivers; marginally in Guizhou. The range is estimated at 8,315 km^2. A rare inhabitant of mesic evergreen forests and shrubs, open habitats and fields (Kaneko 1996b, Luo et al. 2000) in a mountain landscape (1,150–4,000 m a.s.l.).

Characteristics. The smallest member of *Anteliomys*, with a moderately long tail (TL/H&B=0.36–0.43). Fur is shiny and silky, uniformly dull brown to blackish brown above, dark slaty below. Hands and feet are dark brown; the tail is dark brown above, slightly lighter below. The ears are small and strikingly black, therefore contrasting the dorsal fur. Proximal baculum is about 2 mm long and very thick; the lateral distal bones are small and poorly ossified (Zeng et al. 2013). The skull is small, delicate and with a plain lateral profile. Braincase is moderately deep (Figure 106). M^2 is unique in having a prominent postero-lingual salient angle LS4 which is only slightly smaller than LS3. M^3 has 4 inner salient angles in ~75% of cases (Kaneko 1996b) (Figure 107b).

Variation and subspecies. Division into 2 subspecies follows Luo et al. (2000) and Wang (2003).

Anteliomys olitor olitor (Thomas, 1911)

Microtus (Eothenomys) olitor Thomas, 1911c:50. Type locality: “Chao-tung-fu (= Zhaotung Xian; Kaneko 1996b:113), Yunnan. 5800’ [1,770 m]” Thomas 1912d:139), China.

Distribution. North-eastern Yunnan (north-eastern Zhaotong) and western Guizho (Luo et al. 2000).

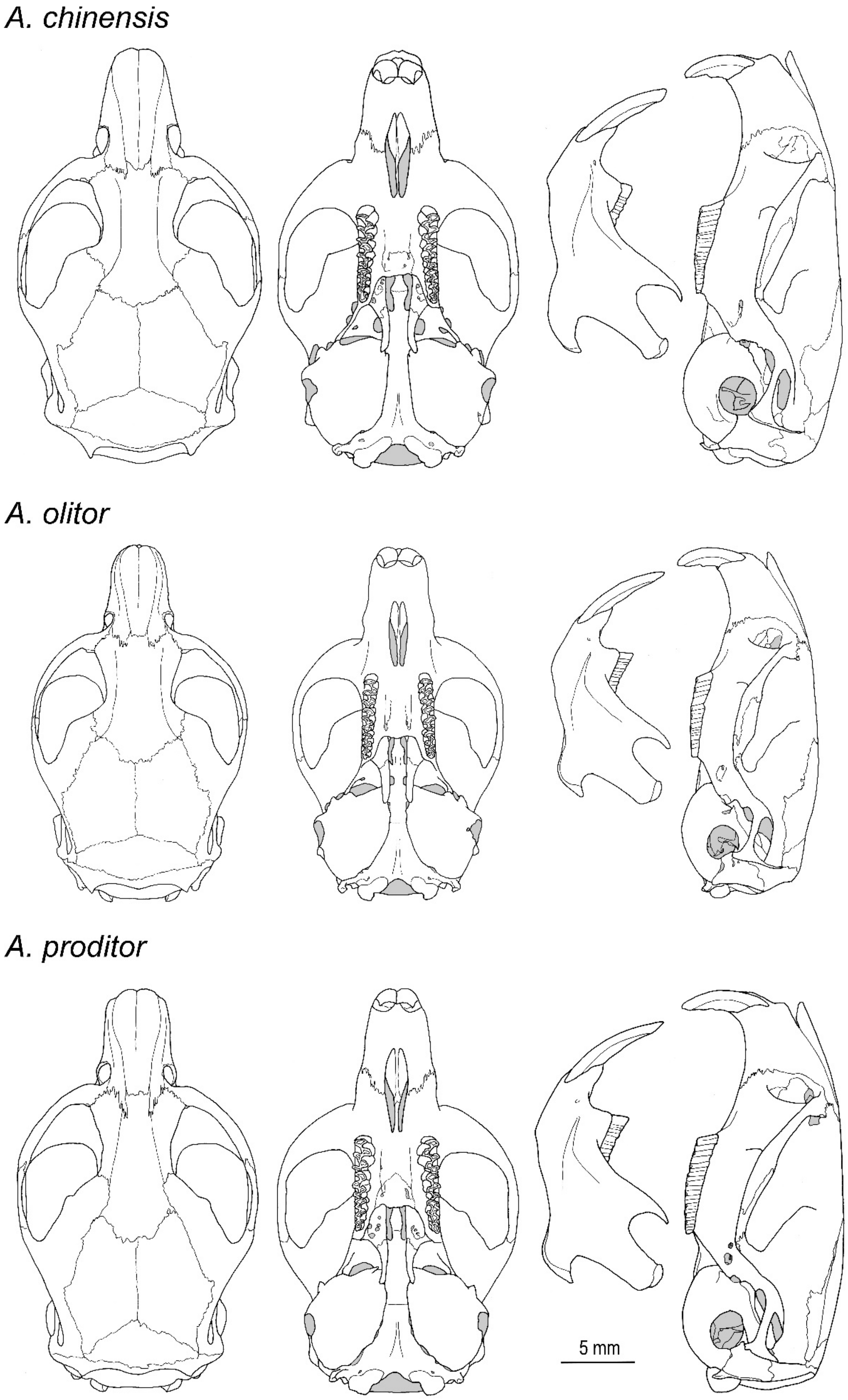


Figure 106: Skull and mandible in Chinese voles (nominotypical subgenus, *chinensis* species group): top–*Anteliomys chinensis* (SW Sichuan, China); middle–*A. olitor* (Zhaotung Xian, Yunnan); bottom–*A. proditor* (Yolungxuen, Yunnan, China).

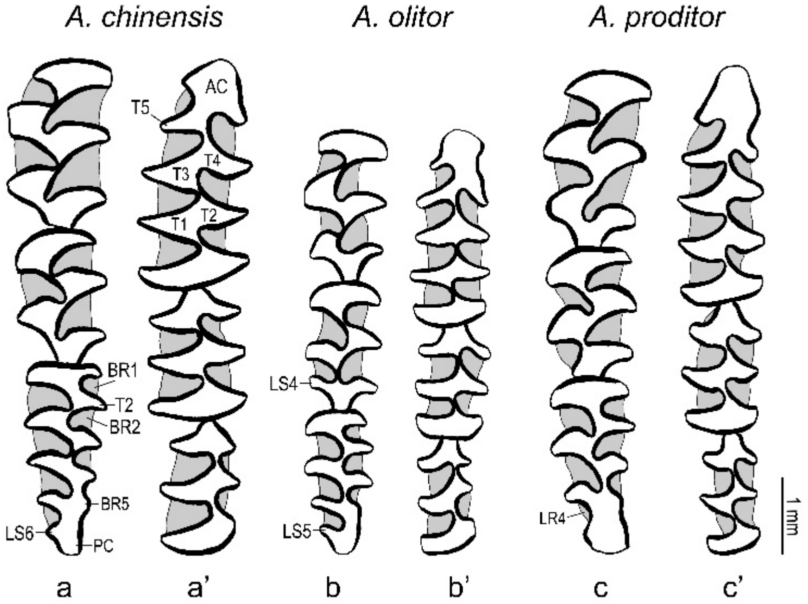


Figure 107: Molar pattern in Chinese voles (nominotypical subgenus, *chinensis* species group). Pictured are upper (a,b,c) and lower rows (a',b',c') in *Anteliomys chinensis* (western Sichuan, China), *A. olitor* (Zhaotung Xian, Yunnan) and *A. proditor* (Lichiang Range, north-western Yunnan, China).

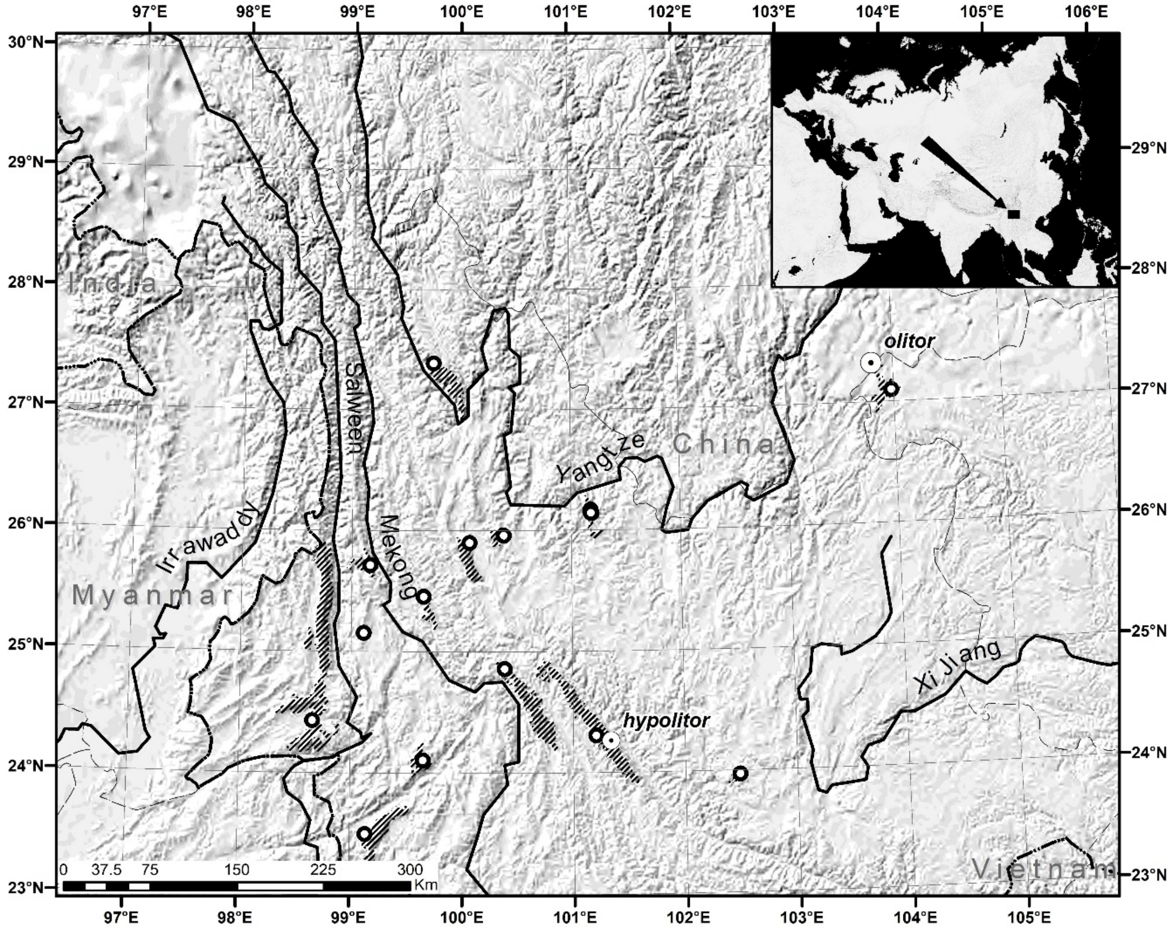


Figure 108: Distributional range of the dwarf Chinese vole *Anteliomys olitor*.

Description. Size small: H&B=82–100 mm, TL=26–39 mm, HF=14–17 mm, EL=9–11 mm, CbL=22.6–24.2 mm, ZgW=13.6–14.2 mm, MxT=5.5–5.8 mm. Bullae are long (7.3–7.6 mm), posteroconid complex >60% the length of M^3 (Luo et al. 2000); tail proportionally longer (TL/H&B=0.26–0.43).

Anteliomys olitor hypolitor (Wang & Li, 2000)

Eothenomys olitor hypolitor Wang & Li (in Luo et al. 2000:397). Type locality: "Yunnan, Jingdong County, Xujiaba (Ailaoshan)", China.

Distribution. Central and western Yunnan: Ailao Mts., Wuliang Mts., Linyi, Baoshan, and Zhongdian (Luo et al. 2000).

Description. Size small: BWt=12–21 g, H&B=78–92 mm, TL=23–32 mm, HF=13–15 mm, EL=7–11 mm, CbL=20.8–22.9 mm, ZgW=12.5–13.7 mm, MxT=4.8–5.7 mm. Bullae are short (4.5–5.3 mm); posteroconid complex <60% the length of M^3 length (Luo et al. 2000); tail proportionally shorter (TL/H&B=0.26–0.36).

Anteliomys proditor (Hinton, 1923) – Yulungshan Chinese Vole

Eothenomys proditor Hinton, 1923:152. Type locality: "Lichiang Range [Yolungxuen; Kaneko 1996b:113], N.W. [north-western] Yunnan, in latitude 27° 30' N. Altitude 13,000' [2,960 m]", China.

Taxonomy. See under *A. olitor*.

Distribution (Figure 109). The northern Yulong Snow Mts. of Likiang on the border between Yunnan and south-western Sichuan. Range is one of the largest in the genus (32,763 km²). Inhabits broad-leaf, coniferous and mixed forests, meadows and open rocky habitats in a subtropical zone and below the timberline (2,400–3,900 m a.s.l.; Allen 1940; Luo et al. 2000). *A. proditor* is widely sympatric with *custos* and marginally sympatric with *hintoni* and *olitor*.

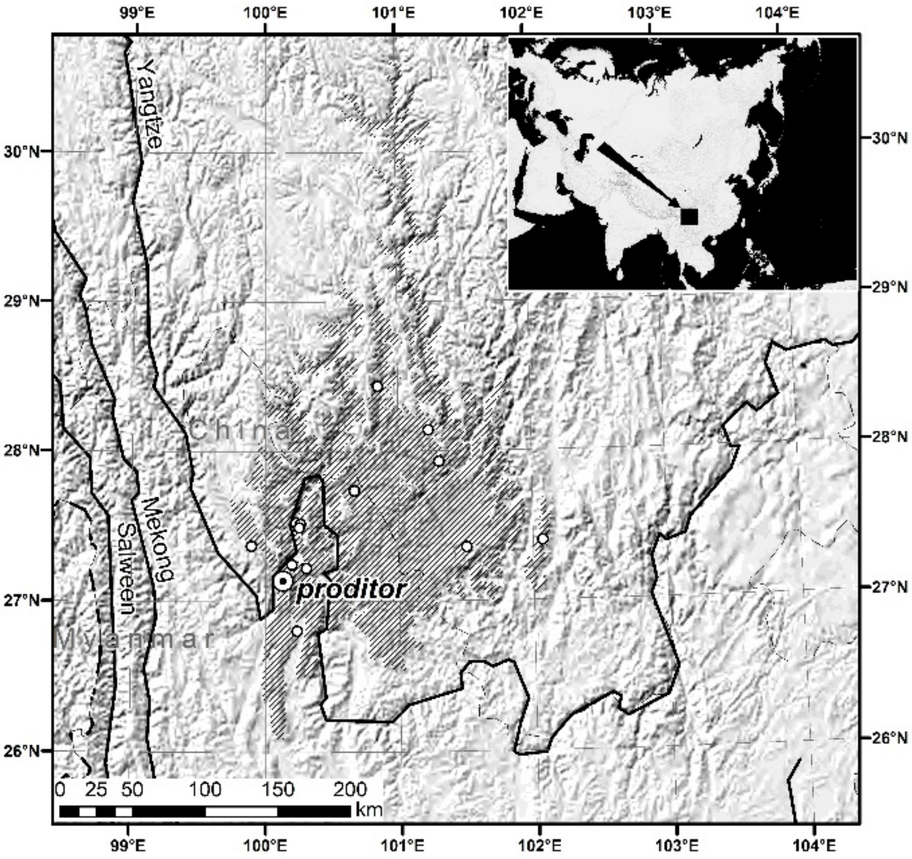


Figure 109: Distributional range of the Yulungshan Chinese vole *Anteliomys proditor*.

Characteristics. Medium-sized and short-tailed species (TL/H&B=0.25–0.40). Dimensions: BWt=26–43 g, H&B=89–110 mm, TL=27–38 mm, HF=16–20 mm, EL=10–14 mm, CbL=25.4–27.9 mm, ZgW=14.5–16.6 mm, MxT=5.3–6.9 mm (Luo et al. 2000). Fur is glossy, smooth and short; uniformly dull-brown above with a rusty tint; the underside is slaty, grizzled with silvery hair tips and washed buff. Hands and feet are blackish brown; the tail is dark brown above, slightly lighter below. Proximal baculum is slender, ~2.1–2.5 mm long; the three distal digits are subequal (Zeng et al. 2013). The skull is large and heavy but only weakly ridged (Figure 106); the interorbital region is wide (4.0–4.7 mm) and flat. Incisive foramina taper posteriorly; bullae moderately long. M^2 lacks postero-lingual salient angle LS4. M^3 has 4 inner salient angles in >80% of cases (Kaneko 1996b); the posterior cap is short (Figure 107c). Karyotype (2n=32, NF=56) consists of 13 pairs of bi-armed and 2 pairs of acrocentric autosomes; the X chromosome is medium-sized submetacentric, whereas the Y chromosome is small and subacrocentric (Li et al. 2006).

Variation and subspecies. Monotypic species. Kaneko (1996b) documented interpopulation variation in size which correlates negatively with altitude.

Species group *wardi*

Anteliomys wardi (Thomas, 1912) – Ward's Chinese Vole

Microtus (Anteliomys) wardi Thomas, 1912c:516. Type locality: "Chamutong [Tra-mu-tang; Kaneko 1996b:113], Upper Salween drainage-area, W.[est] of A-tun-tsi [A-tuntsi]. 13.000' [3,960m]", Yunnan, China.

Taxonomy. Either regarded as a species in its own right or synonymised with *chinensis*. Independent species status confirmed by Zeng et al. (2013) and Liu et al. (2018). *A. wardi* and its sister species *A. custos* diverged ~1.26 Mya (Liu et al. 2018).

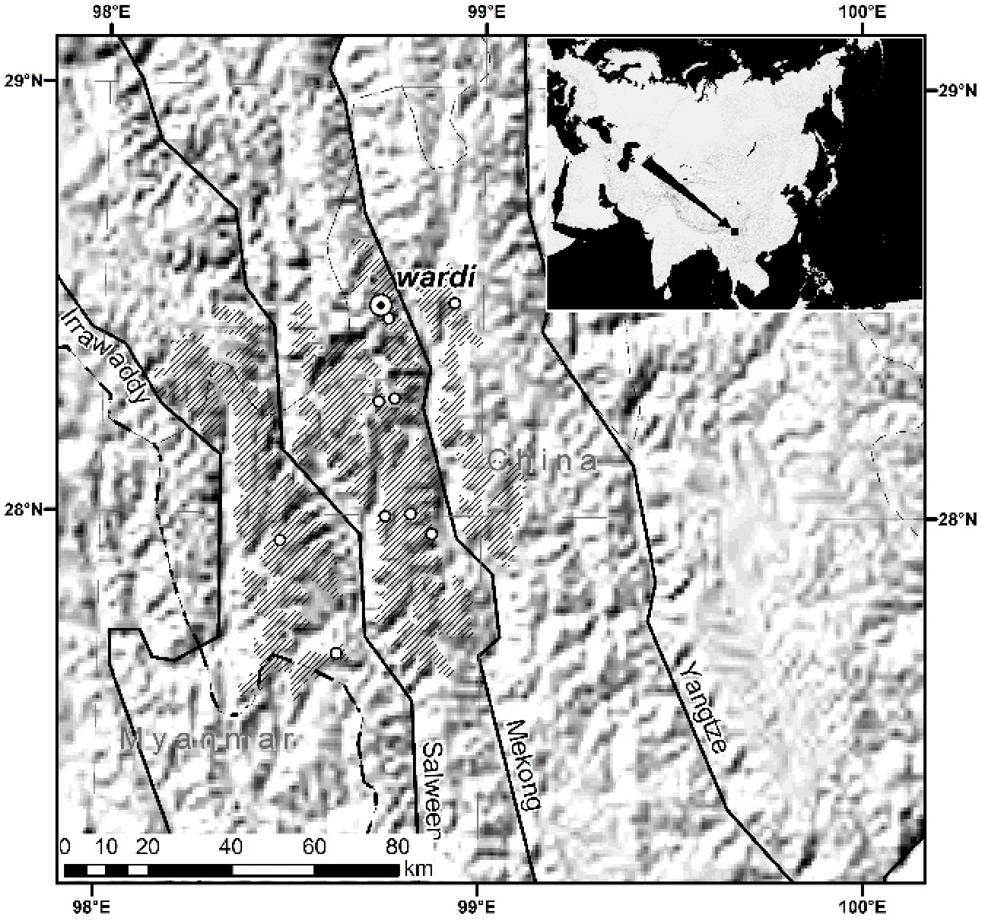


Figure 110: Distributional range of Ward's Chinese vole Anteliomys wardi.

Distribution (Figure 110). Occupies a small range (3,928 km^2) in north-western Dêqên (Yunnan), i.e. on the both banks of the Mekong and Salween Rivers between 27.7° and 28.5° northern latitude. Principal habitats are moist spruce and fir forests, bushes, tall and dense grasslands, alpine meadows and rocky situations at 2,400–4,300 m a.s.l. (Luo et al. 2000). *A. olitor* is broadly sympatric with *custos* and marginally sympatric with *proditor*.

Characteristics. Moderately large and long-tailed species (TL/H&B=0.55–0.85). Dimensions: BWt=22–39 g, H&B=90–108 mm, TL=43–56 mm, HF=17–20 mm, EL=12–15 mm, CbL=23.8–25.3 mm, ZgW=13.8–14.9 mm, MxT=5.1–6.0 mm (Zeng et al. 2013). Ears slightly overtop the pelage. Fur is dense, velvety, approximately 8 mm long; dorsum is grey-brown, underside is lighter, shaded buff in some individuals. Tail is blackish-grey above, light grey below with a pencil of longer hairs at the tip. Feet are grey with 6 plantar pads. Glans penis is unique in having the tip of the urethral lappet with 4–6 forks (up to 4 forks in the remaining species of *Anteliomys*); proximal baculum (length=2.30–2.55 mm) is slender with a wide base; central distal baculum visibly larger than the lateral elements (Zeng et al. 2013). Skull is rather robust and deep with bowed zygomata and weak temporal ridges. Maxillary tooth-rows are markedly apart and diverge posteriorly; bullae are shorter than MxT (Figure 111). M^2 has a blunt postero-lingual salient angle LS4; dental fields T2–T3 are occasionally confluent. M^3 is complex with 5 inner salient angles in approximately 88% of individuals; rarely there are 4 or 6 salient angles (Kaneko

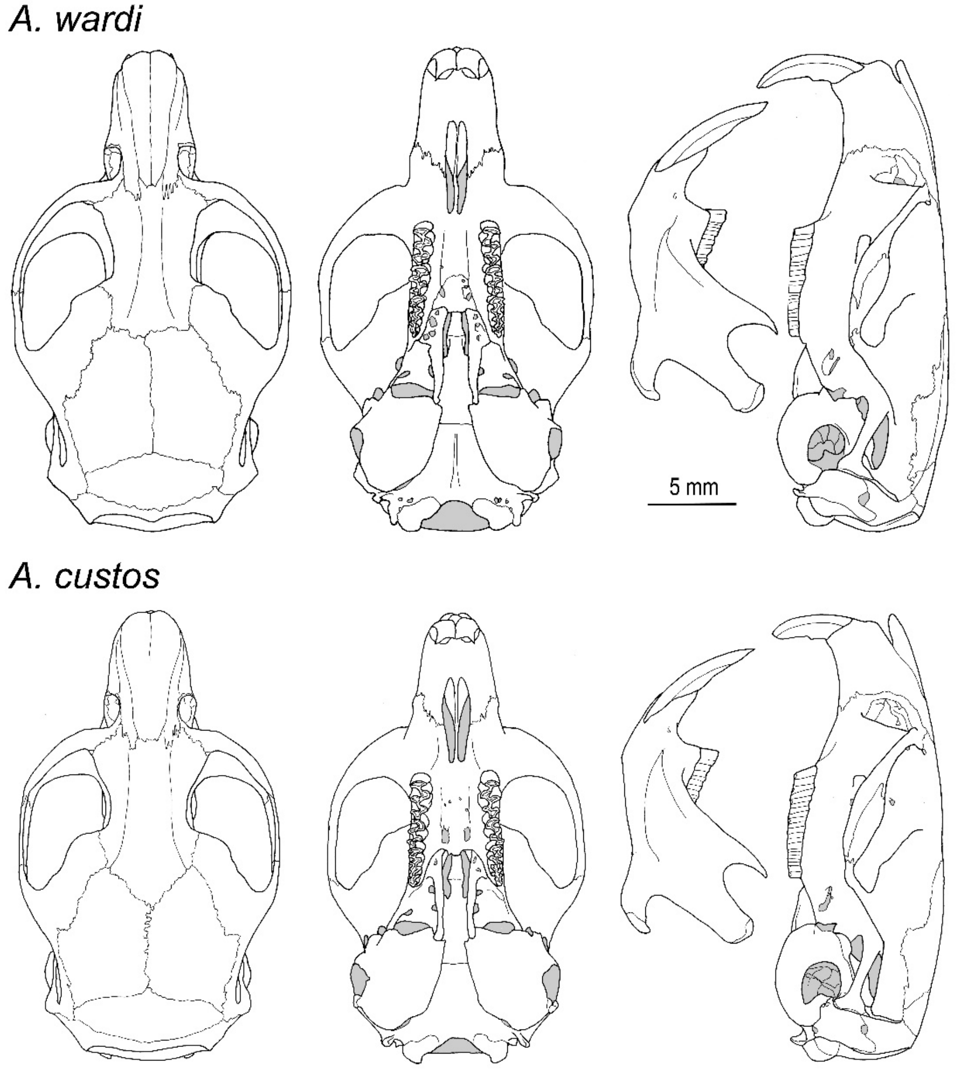


Figure 111: Skull and mandible in Chinese voles (nominotypical subgenus, *wardi* species group): top–*Anteliomys wardi* (Upper Salween drainage-area, Yunnan, China); bottom–*A. custos* (Dêqên, Yunnan, China).

1996b). Buccal re-entrant angle BR2 is much deeper than any other outer re-entrant fold (Figure 112a).

Variation and subspecies. Monotypic species (Luo et al. 2000, Zeng et al. 2013).

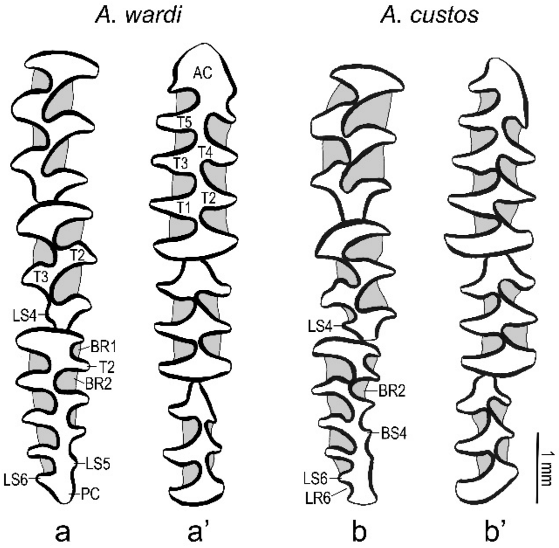


Figure 112: Molar pattern in Chinese voles (nominotypical subgenus, *wardi* species group). Pictured are upper (a,b) and lower rows (a',b') in *Anteliomys wardi* (Upper Salween drainage-area, Yunnan, China) and *A.custos* (Dêqên, Yunnan, China).

Anteliomys custos (Thomas, 1912) – Mountain Chinese Vole

Taxonomy. Until recently *A. hintoni* was treated within the scope of *custos* (Zeng et al. 2013).

Distribution (Figure 113)**.** Mountains east of the Salween River in northern Yunnan and marginally in southern Sichuan. Localities along the southern and western range edge require verification. The range is the largest in the genus (43,634 km^2) and encompasses damp mountain forests, bamboo scrubs, alpine meadows and rocky habitats at 2,500–4,150 m a.s.l. *A. custos* is broadly sympatric with *olitor* and *proditor*, and marginally sympatric with *wardi*.

Characteristics. Size is modest; relative tail length (TL/H&B=0.28–0.53) varies among subspecies. Fur is long and soft, warm brown on the back, more greyish on the head; under surface is paler greyish-brown, occasionally washed with wood-brown. Ears are brown, short and not prominent; feet are drab to grey; tail is drab to dark brown above, whitish to greyish below. Glans penis is unique in having the tip of the urethral lappet with 3 forks; the proximal baculum is sturdy (length=2.25–2.50 mm; Zeng et al. 2013). Skull is smooth and rounded without prominent ridges; interorbital region is broad, short and flat, bullae are small (Figure 111). Transverse bony shelf on the posterior palate carries 2 slight median projections. M^2 has a small, blunt posterior lingual salient angle LS4. In the majority of cases (>90%) M^3 has 5 salient angles on the lingual side (Kaneko 1996b) (Figure 112b).

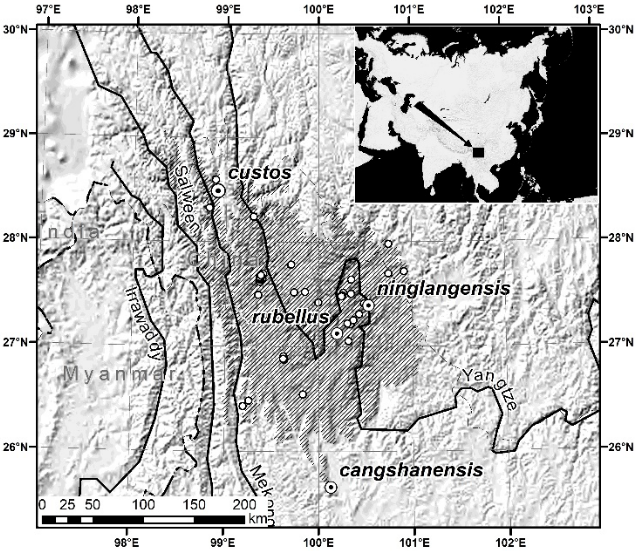


Figure 113: Distributional range of the mountain Chinese vole *Anteliomys custos*.

Variation and subspecies. Following Luo et al. (2000) and Wang (2003), we recognise 4 subspecies; *custos* and *rubellus* were already distinguished as distinct subspecies by Allen (1940).

Anteliomys custos custos (Thomas, 1912)

Microtus (Anteliomys) custos Thomas, 1912c:517. Type locality: "A-tun-tsi [Deqen [=Dêqên] Xian; Kaneko 1996b:112], N.W. [north-western] Yunnan. 11.500–12.500'[3,500–3,810 m]", China.

Distribution. Mountains (altitude >2,700 m) of the north-western part of the range, between the Salween and Mekong Rivers (Zhongdian, Weixi, and Dêqên; Wang 2003).

Description. The smallest subspecies with the relatively longest tail (TL/H&B=0.45). Dimensions: BWt=19–25 g, H&B=85–105 mm, TL=36–48 mm, HF=15–18 mm, EL=10–14 mm, CbL=21.9–25.0 mm, ZgW=12.8–14.2 mm, MxT=5.3–6.3 mm (Luo et al. 2000). Dorsal fur is dark, blackish-brown; belly is washed buff. M^3 has 5 inner and 4 outer salient angles.

Anteliomys custos rubellus (G. M. Allen, 1924)

Microtus (Anteliomys) custos rubellus G. M. Allen, 1924:5. Type locality: "Ssu-shan (Snow Mountain), Li-chiang [Lichiang] range [Yolungxuen; Kaneko 1996b:113], at timber line, 13,000 feet [3,960 m]", Yunnan, China.

Distribution. High altitudes of northern Lichiang (Yunnan).

Description. A large subspecies with a moderately long tail (TL/H&B=0.37). Dimensions: BWt=26–41 g, H&B=93–114 mm, TL=34–49 mm, HF=16–18.5 mm, EL=13–16 mm, CbL=23.7–26.4 mm, ZgW=13.9–15.5 mm, MxT=5.8–6.5 mm. Differs from *custos* in colour: dorsal fur is more reddish and the belly is clear grey (Allen 1940). M^3 with 5 inner and 4 outer salient angles.

Anteliomys custos ninglangensis (Wang & Li, 2000)

Eothenomys custos ninglangensis Wang & Li, 2000 (in Luo et al. 2000:414). Type locality: "Yunnan, north-western Ning-Bo County, Lake Lugu", China.

Distribution. Northern Ninglang (Yunnan) and south-western Muli (Sichuan; Wang 2003) .

Description. A large and short-tailed subspecies (TL/H&B=0.33). Dimensions: BWt=28–39 g, H&B=98–110 mm, TL=29–38 mm, HF=16–20 mm, EL=11–16 mm, CbL=25.1–27.2 mm, ZgW=14.7–16.0 mm, MxT=5.9–6.9 mm. Back is brown to dark brown and belly is whitish grey with buff tint. M^3 has 4 inner and 3 outer salient angles (Luo et al. 2000).

Anteliomys custos changsanensis (Wang & Yang, 2000)

Eothenomys custos changsanensis Wang & Yang, 2000 (in Luo et al. 2000:416). Type locality: "Yunnan, Dali Cangshan", China.

Distribution. Restricted to Mt. Cang (Cangshan) west of Dali City (Yunnan).

Description. A large and long-tailed (TL/H&B=0.47) subspecies. Dimensions: H&B=104–119 mm, TL=45–59 mm, HF=17–19 mm, EL=13–17 mm, CbL=24.2–25.9 mm, ZgW=14.6–15.4 mm, MxT=5.7–6.2 mm. Fur is rather light and belly is whitish-grey. M^2 without the postero-lingual salient angle LS4; M^3 with 5 inner and 4 outer salient angles. (Luo et al. 2000).

SUBGENUS: *Ermites Ermites* S. Liu, Y. Liu, Guo et al., 2012

Ermites S. Liu, Y. Liu, Guo, Sun, Murphy, Fan, Fu & Zhang, 2012 (Liu et al. 2012a:619). Type species: "*Eothenomys hintoni* (as published in the trinomen *Eothenomys custos hintoni* Osgood, 1931 [correctly 1932])".

Taxonomy. Contains 2 small-range species from the mountains of central and southern Sichuan. Both are of moderate size with a tail longer than ½ H&B.

Anteliomys tarquinius (Thomas, 1912) – Sichuan Chinese Vole

Microtus (Anteliomys) chinensis tarquinius Thomas, 1912c:517. Type locality: "23 miles [37 km] S.E. [south-east] of Ta-tsien-lu [Moxi; Kaneko 1996:112], W.[estern] Szechwan [Sichuan]. Alt. 10.000' [3,050 m]", China.

Taxonomy. Described as a subspecies of *chinensis* and until recently treated as such (Hinton 1926a, Allen 1940, Kaneko 1996b, Zhang et al. 1997, Luo et al. 2000, Ye et al. 2002, Musser & Carleton 2005). Liu et al. (2012a) elevated *tarquinius* to a species in its own right and a member of subgenus *Ermites*.

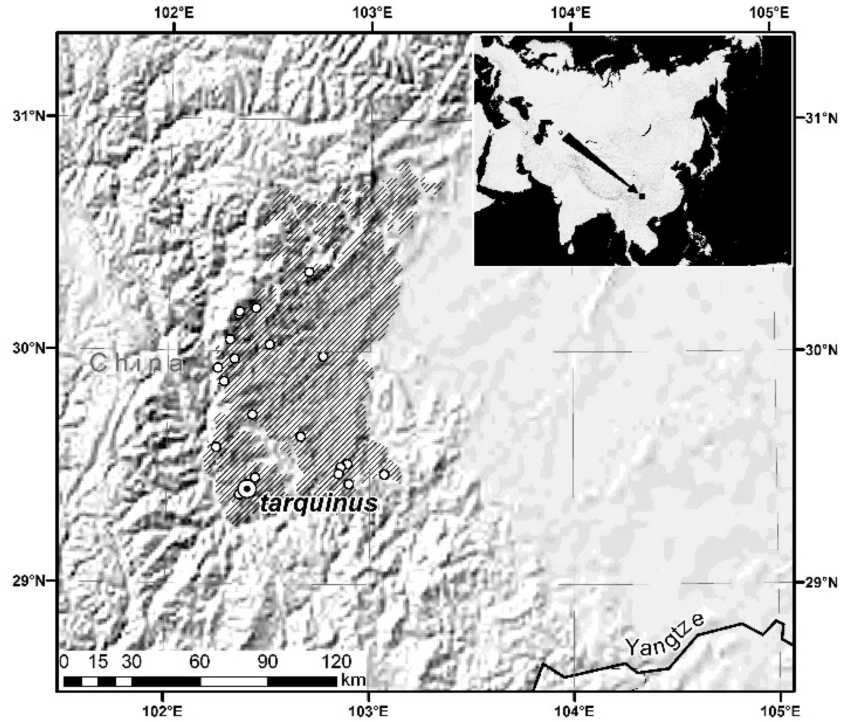


Figure 114: Distributional range of the Sichuan Chinese vole *Anteliomys tarquinus*.

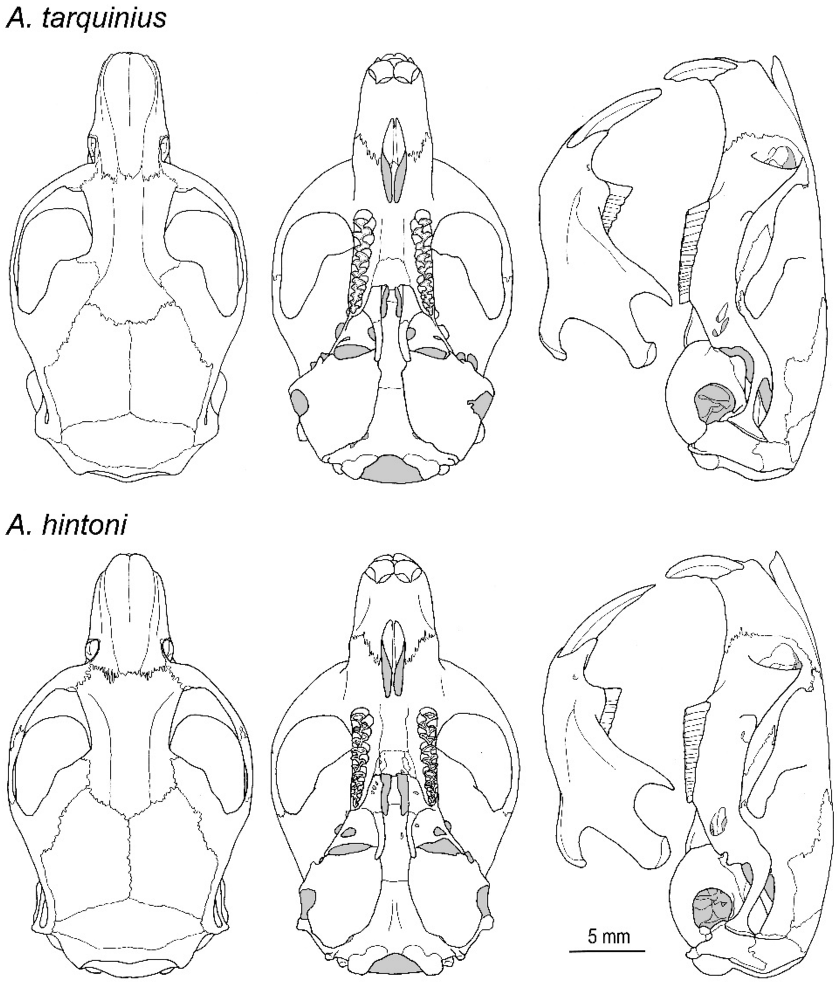


Figure 115: Skull and mandible in Chinese voles (subgenus *Ermites*): top–*Anteliomys tarquinius* (Moxi, Sichuan, China); bottom–*A. hintoni* (Wu-Chi, Sichuan, China).

Distribution (Figure 114). Restricted to the left bank of the Dadu River in central Sichuan, specifically to the counties of Baoxing, Hanyuan, Hongya, Luding, Shimian, Tianquan and Yingjing. The area measures 9,550 km^2, and the altitudinal range is 1,400–3,400 m.

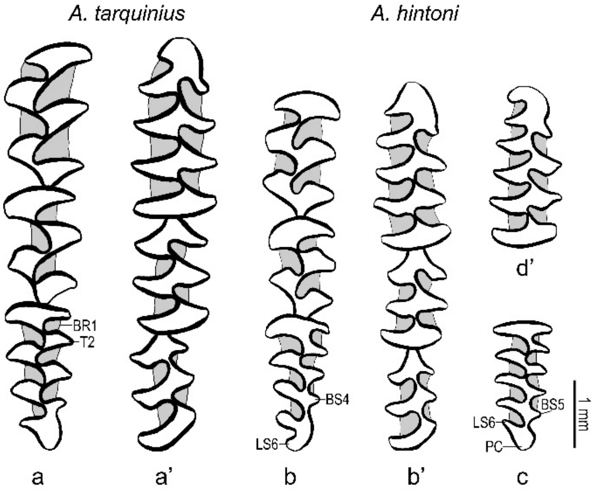


Figure 116: Molar pattern in Chinese voles (subgenus *Ermites*). *Anteliomys tarquinius:* upper (a) and lower rows (a'; Moxi, Sichuan, China). *A. hintoni:* upper (b) and lower rows (b'; (Wuxu, Sichuan, China); isolated M^3 (c–Jinyang County, Sichuan) and M$_1$ (d'–Meigu County, Sichuan).

Characteristics. A moderately large and long-tailed species (TL/H&B=0.50–0.75). Dimensions: H&B=102–122 mm, TL=59–76 mm, HF=19–24 mm, EL=13–17 mm, CbL=25.6–28.7 mm, ZgW=13.7–16.0 mm, MxT=5.5–6.9 mm (Liu et al. 2018). Fur is dense and velvety, deep brown to dull brown with brassy reflection, belly is bluish grey; the demarcation on flanks is indistinct. Feet covered with short greyish hair; ears are grey to blackish grey. The tail is blackish brown above, grey below. Glans penis is on average 4.06 mm long and 2.06 mm wide. The urethral lappet has 2 forks. Length of proximal/distal baculum is 1.57/1.16 mm (Liu et al. 2018). Skull is rather narrow (ZgW/CbL=0.52–0.59), angular with prominent ridges and squamosal protuberance; nasals are long and their posterior edge is at the level of posterior expansion of the nasal process of the premaxilla. Braincase is long; incisive foramina broadly oval and the posterior edge of the hard palate has a prominent medial spine (Figure 115). M^3 has 4–5 salient angles on both sides; the posterior cap is small and very short. M$_1$ is simple; dental field of T5 widely communicates with the anterior loop (Figure 116a).

Variation and subspecies. Monotypic species.

Anteliomys hintoni Osgood, 1932 – Hinton's Chinese Vole

Taxonomy. Liu et al. (2012a) showed that *hintoni*, which was treated as a subspecies of *custos*, is a species in its own right. Subsequently, Liu et al. 2018) named 3 cryptic species which closely relate to *hintoni*; we treat them as subspecies.

Distribution (Figure 117). Range is of moderate size for the genus (25,154 km^2) and covers the southern Garzê Tibetan and Liangshan Yi districts of southern Sichuan. Preferred are mesic habitats with a deep layer of humus and abundant mosses, tall-grassy meadows, azalea and bamboo shrubs and coniferous woodland at high altitudes (2,450–4,150 m). *A. hintoni* is marginally sympatric with *A. proditor* and *chinensis*.

Characteristics. Size is modest but varies among subspecies. Tail is relatively long (TL/H&B=0.50–0.65). Fur is long (8–12 mm) and soft; back is greyish-brown and washed along the spine with wood-brown; muzzle is pale drab-brown and underside is greyish-brown. Ears are grey or brown, densely covered by hair; fore and hind feet are drab-white. The tail is distinctly bi-coloured, dusky above, lighter below; although densely clad with stiff hair, the underlying annulation is not hidden. Glans penis shows no peculiarities; length ($\bar{x}$±SD)=3.65±0.26 mm (ssp. *jinyangensis*) and 4.24±0.36 mm (*meiguensis*). Urethral lappet has 2–4 fingerlike processes; the central 1–2 processes are usually small. Mean length of proximal baculum varies between 2.20±0.20 mm (*luojishanensis*) and 2.56±0.13 mm (*hintoni*). Medial distal baculum is 1.3–1.4-times the length of the lateral digits (Liu et al. 2018). Skull is rather narrow (ZgW/CbL=0.52–0.59); nasals are short. Incisive foramina are short and broadly oval (Figure 115). M^3 is complex with 4–6 (usually 5) salient angles on each side; the posterior cap is very long. M$_1$ is of a fairly simple structure; dental field T5 is long and communicates with the anterior loop (Figure 116b-c).

Variation and subspecies. Subspecies are well-defined by molecular markers (Liu et al. 2018). For spelling of the author's name (Liu instead of Shaoying) for 3 subspecies names see comment under *Eothenomys eleusis shimianensis*.

Anteliomys hintoni hintoni (Osgood, 1932)

Eothenomys (Anteliomys) custos hintoni Osgood, 1932:321. Type locality: "Wushi [Wuxu; Kaneko 1996b:112], southwest of Tatsienlu, Szechwan [Sichuan], China. Altitude 12,000 feet [3,660 m]".

Distribution. North-western part of the range in Daxue Mts. (between the Dadu and Yalong Rivers) in southern KangDing, JiuLong, north-western MianNing, and western ShiMian counties.

Description. The largest subspecies with the longest tail (TL/H&B=0.48–0.63). Dimensions: H&B=92–120 mm, TL=47–60 mm, HF=17–21 mm, EL=13–16 mm, CbL=23.1–25.8 mm, ZgW=12.4–14.3 mm, MxT=4.7–5.8 mm. Dorsal fur is dull brown, occasionally shaded buff; belly is grey, transition on flanks distinct. Urethral lappet with 2 forks. M^3 has 5 inner salient angles in 62% of individuals; the remainder have 4 angles; the outer side usually (~80% of cases) with 4 salient angles, rarely with 5 (Liu et al. 2018).

Anteliomys hintoni jinyangensis (Liu, 2018)

Eothenomys jinyangensis Liu, 2018 (in Liu et al. 2018:15, Figs. 7A & 8A). Type locality: "Baicaopo Nature Reserve, Jinyang county, Liangshan Canton, southwestern Sichuan, China, 103.275°N, 28.700°E, elevation 3490 m."

Distribution. High altitudes (>3000m) in the eastern part of Liangshan Yi Autonomous Prefecture, south-western Sichuan.

Description. The smallest subspecies with a proportionally short tail (TL/H&B=0.40–0.59). Dimensions: H&B=85–105 mm, TL=40–54 mm, HF=16–20 mm, EL=13–17 mm, CbL=21.6–24.1 mm,

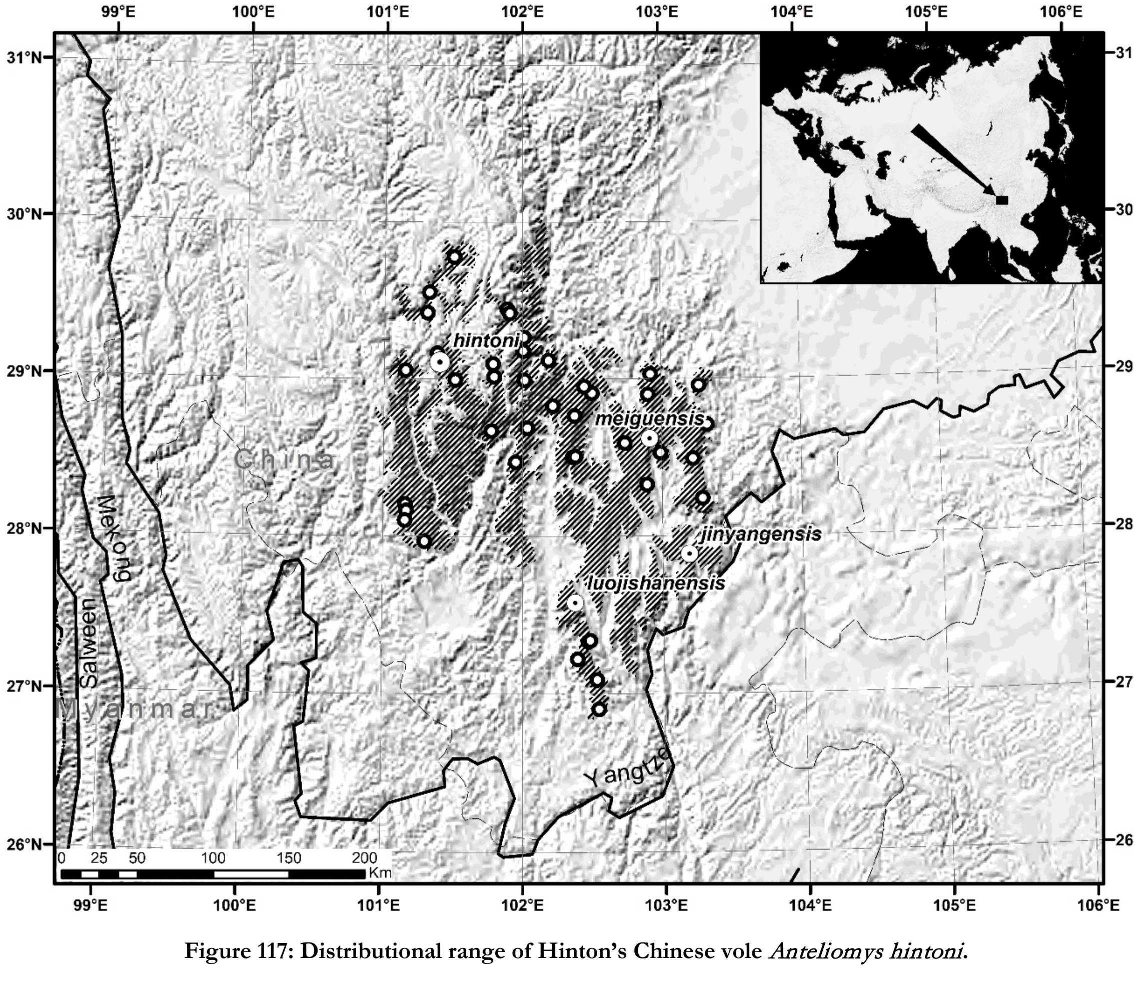


Figure 117: Distributional range of Hinton's Chinese vole *Anteliomys hintoni*.

ZgW=11.2–13.8 mm, MxT=4.4–5.2 mm (Liu et al. 2018). Back fur is grey, sometimes shaded buff; belly is lighter, transition along the flanks gradual. Urethral lappet with 3–4 forks. M^3 has 5–6 inner salient angles and 6 outer angles in ~50% of cases; 4 outer angles are rare (in 5% of cases).

Anteliomys hintoni meiguensis (Liu, 2018)

Eothenomys meiguensis Liu, 2018 (in Liu et al. 2018:22, Figs. 7B & 8B). Type locality: "Lanlong region of Dafengding National Nature Reserve, Meigu county, Liangshan Canton, southwestern Sichuan, 28.62169°N, 102.9119°E; elevation 3020 m", China.

Distribution. Bibo and Dafengding Mts. (altitude=2,560–3,850m) in the counties of Yuexi, Mabian, Meigdu, Mianning, Shimian, Ganluo, Yuexi, Ebian, and Zhaojue (Liu et al. 2018).

Description. Small subspecies with a proportionally short tail (TL/H&B=0.42–0.56). Dimensions: H&B=90–110 mm, TL=39–55 mm, HF=16–19 mm, EL=12–15 mm, CbL=22.0–24.1 mm, ZgW=12.5–13.9 mm, MxT=4.8–5.4 mm. Dorsal fur is brown, belly is grey and demarcation is abrupt. Urethral lappet with 2–3 forks. Skull more angular with prominent squamosal protuberance. M^3 has 5–6 inner angles and 4–6 outer angles (in >50% of cases there are 4 angles; Liu et al. 2018).

Anteliomys hintoni luojishanensis (Liu, 2018)

Eothenomys luojishanensis Liu, 2018 (in Liu et al. 2018:25, Figs. 7C & 8C). Type locality: "Luojishan Nature Reserve, Puge County, Liangshan Canton, southwestern Sichuan, 27.578903°N, 102.374423°E; elevation 3680 m", China.

Distribution. High altitudes (>3,000m) in the Luoji Mts (counties of Dechang, Puge, Ningnan, and Miyi).

Description. Size moderate, tail moderately long (TL/H&B=0.43–0.59). Dimensions: H&B=95–108 mm, TL=46–58 mm, HF=17–18.8 mm, EL=12–15 mm, CbL=22.9–25.0 mm, ZgW=12.5–14.0 mm, MxT=4.8–5.7 mm. Back fur is grey, lighter on belly, gradual transition along the flanks. Urethral lappet with 3 forks. M3 with 5 inner and 4–5 outer angles (Liu et al. 2018).

TRIBE:
Arvicolini Gray, 1821

SUBTRIBE:
Bramina Miller & Gidley, 1918

Braminae Miller & Gidley, 1918. Type genus is *Bramus* Pomel, 1892.

Synonyms. Ellobiinae Gill, 1872; Ellobii Weber, 1928; Ellobiini Simpson, 1945; Ellobiusini Pavlinov et al., 1995.

Taxonomy and nomenclature. The family group name Ellobiinae Gill, 1872, is a junior homonym of Ellobiini Pfeiffer, 1854 (Gastropoda, Mollusca), and is therefore preoccupied. Pavlinov et al. (1995) emended Ellobiini Gill to Ellobiusini. As stipulated by the Code, an emendment is justified when it replaces an incorrect spelling of the name. Because Ellobiini Gill is the correct name, the emendation made by Pavlinov et al. (1995) is an unjustified emendment of an available name (Arts. 19.2 and 33.2). In accordance with the Code, Ellobiusini is an available name but is a junior objective homonym of Ellobiini Gill (Arts. 19.1 and 33.2.3). Ellobiini Gill must be replaced by the next oldest available name from among its synonyms (Art. 39 of the Code) which is Braminae Miller & Gidley, 1918. The name is mandatorily emended to Bramina for the extension to match the subtribal rank.

Early authors, puzzled by the extreme adaptations of mole-voles for a subterranean existence, classified these arvicolines together with unrelated fossorial rodents which are now in the families of mole-rats (Spalacidae) and blesmols (Bathyergidae). Kerr (1792) assigned mole-voles to *Myotalpa*, Schreber (1792) to "Mures subterranei", and Illiger (1811) to *Georychus*. Fischer (1814) defined *Ellobius* in a similarly broad concept inside the family "Spalacoidum". Later students continued to link mole-voles with blesmols (Bonaparte 1845) or mole-rats (Giebel 1855, Carus 1868, Miller & Gidley 1918). Palmer (1897) was the first to regard *Ellobius* as a member of Microtinae (=Arvicolinae), which was endorsed by Hinton (1926a) and the vast majority of later authors. *Ellobius* is also unique in aspects of its morphology not directly related to burrowing habits (cf. Hooper & Hart 1962). This caused Gromov (in Gromov & Polyakov 1977) to assign mole voles to true hamsters (subfamily Cricetinae) but his view persuaded few authors. Inside Arvicolinae, mole voles were usually ranked as a tribe Ellobiini or more rarely as a subfamily either named Ellobiinae (of Arvicolidae; Kretzoi 1955), or Braminae of Rhyzomyidae (Miller & Gidley 1918); Rhyzomyidae currently rank as a subfamily of Spalacidae. Although molecular reconstructions unequivocally placed *Ellobius* into Arvicolinae, they failed to retrieve its exact phylogenetic position.

According to many authors (e.g. Robovský et al. 2008, Bondareva et al. 2020), *Ellobius* emerged as the basal group of arvicolines. More likely, however, the mole voles originate from the 2nd radiation of Arvicolinae as an early offshoot of Arvicolini (Steppan & Schenk 2017) and are possibly a sister group to Lagurina. We therefore amend the rank of mole-voles to a subtribe inside Arvicolini. TMCRA for *Ellobius* and *Microtus* is estimated at 4.85–5.23 Mya (CI=4.20–5.88 Mya; Lebedev et al. 2020). Mole voles appeared in the fossil record during the Late Pliocene (Topachevskiy & Rekovets 1982, Tesakov 2008).

Extant mole voles split into 2 main branches which were classified as species groups (*talpinus* and *fuscocapillus* groups; Ellerman 1941) or more recently as two subgenera (the nominotypical *Ellobius* and *Afganomys*; Topachevskiy 1965). The fossil record of each group extends to the Early Pleistocene but the lineages possibly diverged in the Late Pliocene (Tesakov 2016); the molecular clock estimate is 3.32–3.69 Mya (CI=2.82–4.26 Mya; Lebedev et al. 2020). During their long independent evolution, the 2 groups accumulated apomorphies in craniodental traits (Topachevski 1965, Tesakov 2008, 2016), nucleotide sequences (Lebedev et al. 2020) and karyotypes. Among others, the proportion of thymine at the 3rd position of nucleotide sequences is lower in *Ellobius* than in *Bramus* (Lebedev et al. 2020). In the stomach, *Ellobius* has a shallower *incisura angularis* and a lower proportion of glandular epithelium than *Bramus* (Vorontsov 1962, Carleton 1981). Major steps in the evolution of heterosomes (translocations of Y chromosome fragments carrying a few male-specific genes and, finally, a loss of Y) were achieved independently (Bakloushinskaya & Matveevsky 2018) and comparative chromosome painting of *talpinus* (*Ellobius* s.str.) and *lutescens* (*Bramus*) retrieved a number of rearrangements from the ancestral karyotype (Romanenko et al. 2007). Pozdnyakov (2008) argued that *Bramus* should merit a rank of genus in its own right, which is followed here. The name *Afganomys* is a junior synonym of *Bramus*, which was established on the Pleistocene material from northern Africa (Tesakov 2016).

Distribution. Steppes, semideserts, true deserts and mountain meadows between Dnepr (Ukraine) and central Nei Mongol (China), and from 56^0 northern latitude in Russia southward to 26^0 in Sistan and Baluchestan (Iran).

Characteristics. Small to moderately large subterranean voles. Body is cylindrical and the tail is very short (usually TL/H&B<0.10); the neck is barely present. Head is large with short and bluntly rounded muzzle. The proodont incisors are exposed in front of the mouth even when the lips are in a normal closed position (Figure 118). Rhinarium is big and hard, surrounded by short, stiff whiskers. Contrary to other arvicolines, the *alae nasi* and the infra-narial portion extend ventrally, reaching the gum and the upper incisors (Figure 119). Lateral lobes of the upper lip are more progressively developed than in any other arvicoline group; the left and right lobes are fused to each other across the mid-line (Vinogradov 1926). Eyes are minute; in *E. talpinus*, the diameter of the eyeball is 3.2 mm and its mass equals 0.06% of total body mass (Popov 1960). Pinnae are reduced to a small triangular projection, 2–3 mm high. The tail is short, covered by stiff hairs ending in a long thin terminal pencil. Front feet are nearly the same length as hind legs (Figure 120) while they are evidently shorter in other arvicolines. Feet are broad and robust; palms and soles are naked with 5 palmar and 6 plantar pads. Palmar pads are small and the metatarsal pair tends towards reduction. The thumb is short but otherwise normally developed; fingers II and III are the longest. Claws are short and blunt, rarely long. Borders of palms, soles, toes and the outer borders of the forearm are fringed with stiff hairs. Fur is moderately long, dense and fluffy since it almost completely lacks stiffer guard hairs (Allen 1940); hairs are short on the head and muzzle. Colour varies from light grey or sandy-grey to black; the top of the head is normally darker than the back and the ventral side can have white stripes or irregular patches (e.g. in *tancrei* and *lutescens*). Hair bases are invariably slate. Young are grey all over with a dark muzzle. The posterolateral glands are absent (Quay 1968). Females have 2 pairs of pectoral and 1 pair of inguinal nipples (6 nipples in total; Thomas 1895, Davydov 1988; I. Bakloushinskaya personal information). The stomach and the caecum are disproportionally small and the intestine length in *E. talpinus* is only 3.5–4.7-times that of the length of the head and body; this is significantly less than in the majority of arvicolines (Vorontsov 1962, Naumova et al. 2018). Bramina is also unique among arvicolines in having 2 transverse diastemal ridges on the dorsal side of the oral cavity (reported in *Ellobius tancrei*; Quay 1954).

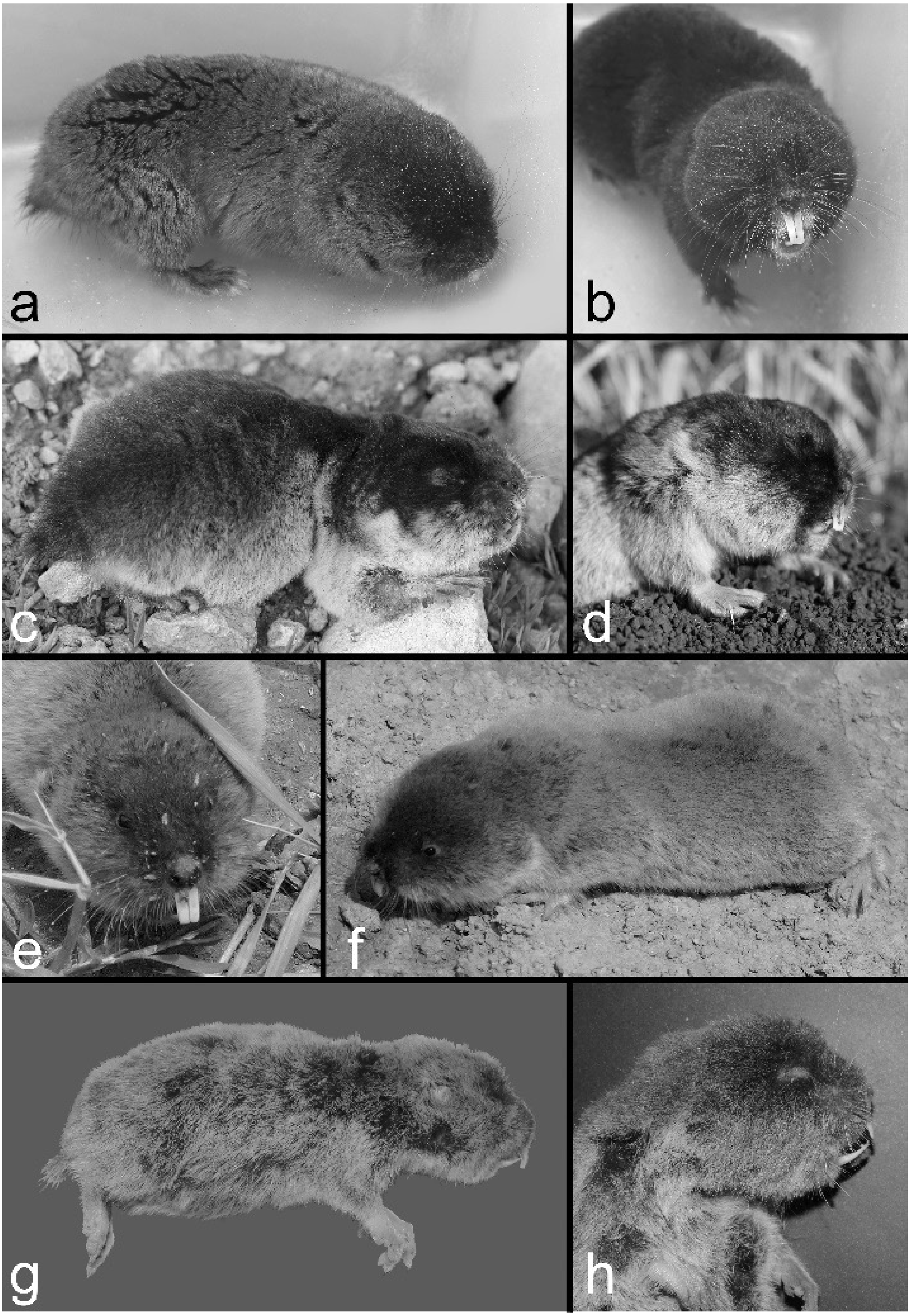


Figure 118: Representative species of mole voles. a,b,c–*Ellobius talpinus talpinus:* "brown" (a), "black" (b) and "intermediate" (c,d; Tatarstan (Russia) colour morphs; brown and black animals are from southern Kurganskaya Oblast, central Ural Mts. e,f –*E. tancrei alaicus* from Alai Valley, Kyrgyzstan. g,h–*Bramus lutescens* from Iran. Photo courtesy Dina Nesterkova (a,b), Irina Bakloushinskaya (e,f) and B. Kryštufek (c,d,g,h).

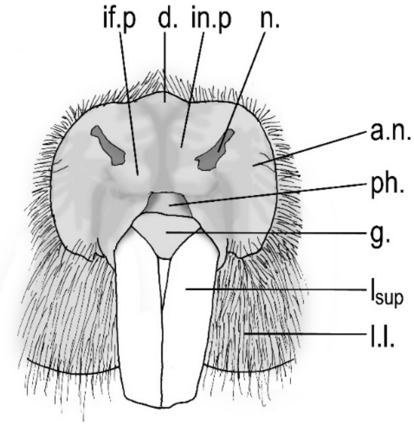


Figure 119: Rhinarium in *Bramus lutescens* (from Arak, Iran). I_{sup}–upper incisor; a.n.–*ala nasi*; d–dorsum; g–gum between the upper incisors in.p.–internarial portion*;* if.p.–infranarial portion; l.l.–labial lobe; n–nares (external nostrils); ph–philtrum.

The most obvious peculiarity on the skull are the exceptionally proodont incisors (Figures 121 & 125). The skull is wedge-shaped in the profile view with a weakly inclined occipital region. Zygoma are thick and widely expanded (ZgW/CbL>0.67), interorbital region is wide, the brain-case is pear-shaped and the rostrum is long and slender. The post-orbital projections on the squamosal are slight. Infraorbital foramen is oval and almost completely lacks the outer wall; its ventral portion for nerve transmission is closed (slit-like in other arvicolines), and the upper portion for transmission of the medial masseter is enlarged. Incisive foramina are very short and bullae are small. Hard palate is of *Microtus* type and the posterior margin is either continuous or broken up (Figure 10e); choanae are separated by a narrow to moderately broad medial septum: the lateral fossae are deep. Mandible has a high recurved coronoid process, a heavy articular process, and a short, blunt angular process. Incisors are lengthened and levelled. Roots of upper incisors extend back, having the alveolar capsule at the level of M^1; the lower incisors form an additional (alveolar) process on the labial side of the ramus mandibulae. Molars are rooted with 1 (3rd molar) and 2 roots (1st and 2nd molars), respectively. Re-entrant angles lack cement. The enamel is not differentiated and consists of radial elements; lamellar enamel is present on the apices of salient angles but the tangential enamel is absent (Koenigswald 1980). Dental fields are widely confluent and the angles are rounded. Molar pattern wears out with age and the angles obliterate. M^1 consists of the same elements as in other arvicolines; M^2 has 3–4 triangles and the M^3 has 2–3 triangles between the anterior lobe and the posterior cap. The M_1 has 3–4 re-entrant angles lingually and 2–3 labially; M_2 is with 2 deep re-entrant angles on each site and M_3 has 2 re-entrant angles on the lingual and 1–2 on the labial side. Opposite salient angles of M_2 are widely confluent and do not alternate (Figures 122 & 126).

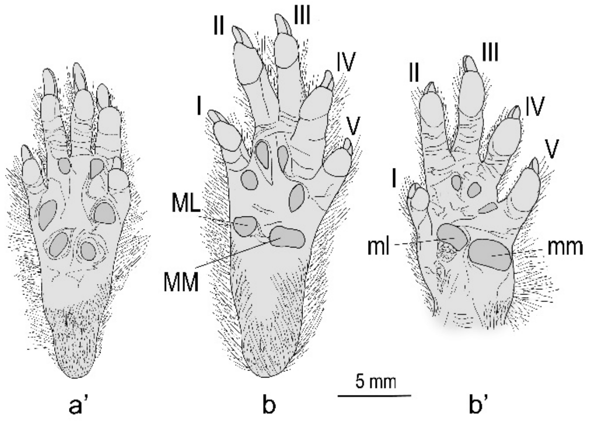


Figure 120: Left sole (a,b) and palm (b') in *Elobius talpinus* (a; Saratov Oblast, Russia) and *Bramus fuscocapillus* (b,b'; Afghanistan).

Key to genera and species

1a) Posterior end of premaxillary approximately at the level of the naso-frontal suture; interparietal present; incisive foramina approximately of the same length as M^1; M^2 with 2 lingual salient angles …........ 2 (*Ellobius*)

1b) Posterior end of premaxillary lies caudally to the naso-frontal suture; interparietal absent in subadults and older; incisive foramina much shorter than M^1; M^2 with 3 lingual salient angles …………………….. 3 (*Bramus*)

2a) M^3 usually as long as it is wide, of simple structure, with 2 labial salient angles and a poorly developed heel; karyotype consists entirely of acrocentrics ……………………..…………………… *E. talpinus*

2b) M^3 longer than it is wide, of complex structure, usually with 3 labial salient angles and an elongated heel; karyotype contains at least 1 bi-armed pair ……………………………………………... *E. tancrei*

3a) Pelage usually dull without bright tint; cheeks of same colour (dark wood-brown) as the top of the head; sagittal crest does not reach the lambdoid crest; 2n=17 ……………………………………..… *B. lutescens*

3b) Pelage usually light, occasionally bright; cheeks lighter (usually buff) than the top of the head (usually dark wood-brown or blackish-brown); sagittal crest reaches the lambdoid crest; 2n=36 ………………………….......................... *B. fuscocapillus*

GENUS: *Ellobius* Fischer, 1814 – Northern Mole Voles

Ellobius Fischer, 1814:72. Defined as a genus in the family "Spalacoidum" (= Spalacidae). Type species by subsequent designation (Ellerman 1941:639) is *Mus talpinus* Pallas.

Synonyms. *Chthonergus* Nordmann, 1840; *Lemmomys* Lessone, 1842:123.

Taxonomy. Ellobius s str. was still considered monospecific in the mid-20th century (Ognev 1950, Ellerman & Morrison-Scott 1951). Topachevskiy (1965) delimited *tancrei* and *talpinus* and diagnosed them via M^3 morphology. At approximately the same time Vorontsov et al. (1969) defined karyological differences between them, although still presuming that the variation is an intraspecific phenomenon. Since the 1980s a tripartite taxonomy (*talpinus, tancrei, alaicus*) was adopted and has remained in use to the present. Lebedev et al. (2020) however, showed that basal division into 2 major lineages (*talpinus* and *tancrei;* TMRCA=0.44–0.53 Kya) was proceeded at the end of the Middle Pleistocene (~220–230 Kya) by a nearly simultaneous split into 3 sublineages (*talpinus*) and 2 lineages (*tancrei*), respectively. *E. tancrei* is paraphyletic with respect to *alaicus* which originated at the Middle/Late Pleistocene boundary (~120–140 Kya).

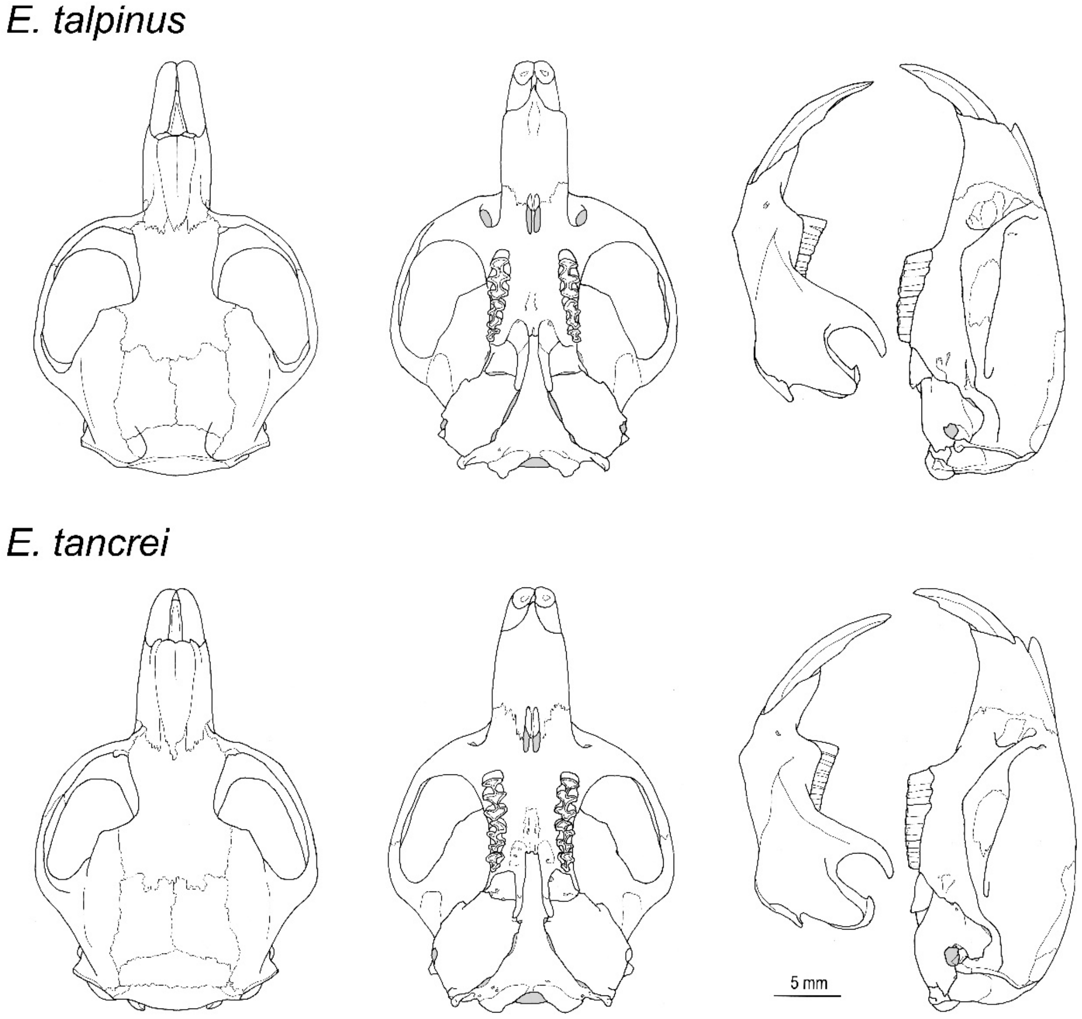


Figure 121: Skull and mandible in northern mole voles *Ellobius* (top-to-bottom): *E. talpinus* (Tatarstan, Russia) and *E. tancrei* (Nookatskyi Balkash, Kyrgyzstan).

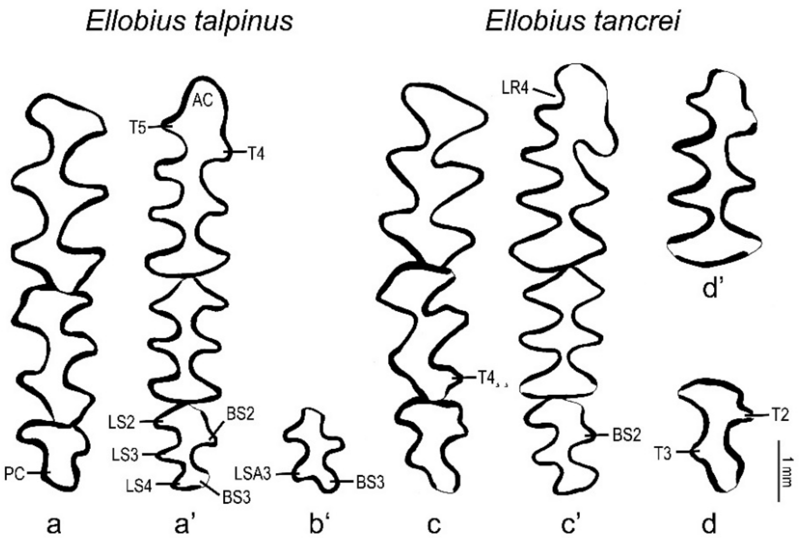


Figure 122: Grinding pattern on upper (a,c) and lower molar rows (a',c') and isolated M^3 (d), M_1 (d') and M_3 (b') in northern mole voles *Ellobius*. a–*E. talpinus kashtschenkoi* from Tatarstan, Russia; b'–*E. talpinus orientalis* from Dorngovi Amag, East Gobi, Mongolia; c–*E. tancrei fuscipes* from Juchsu, Tajikistan; d,d'–*E. tancrei alaicus* from Osh Region, Kyrgyzstan.

These results suggest 6 allopatric species of *Ellobius* which at present are insufficiently defined. We therefore restore a conservative 2-species division.

Interspecific crosses between *talpinus* and different karyomorphs of *tancrei* yielded non-viable F1 hybrids (Bakloushisnkaya et al. 2012). Hybrids between *tancrei* and *alaicus* were documented in nature (Bakloushinskaya et al. 2019) and reproduced in captivity. On the other hand, the intraspecific hybrids between different cytotypes of *tancrei* (e.g. 2n=34×54) are fertile (Bakloushinskaya et al. 2012).

Distribution. The subgenus occupies the northern portion of the mole voles' range, as far south as ~35° northern latitude. The ranges of the 2 species are allopatric with some parapatry in Turkmenia and central and north-eastern Kazakhstan (Yakimenko 1984, Bakloushinskaya et al. 2012).

Characteristics. Size is smaller on average than in *Bramus*. The glans penis is short (⅓ the length of the distal tract of the penis) and wide. The skin on the surface is gathered into thick longitudinal folds; there are no spines. The baculum is a small (1.5-times the glans length), simple bone which has an expanded base and a stalk-like distal part; there is no trident (Ognev 1950, Hooper & Hart 1962). Temporal ridges remain weak and do not fuse into a sagittal crest. The premaxilla does not expand behind the naso-frontal suture and the line of lacrimals. The parietal bone is present. Incisive foramina are longer than in *Bramus*, equalling the length of M^1. Zygomatic arches are set more ventrally than in *Bramus* and the upper incisors are shorter (Figure 121). M^2 has 3 triangles; M^3 has at most 2 blunt salient angles between the anterior lobe and the rudimentary posterior cap. The anterior cap of M_1 is widely confluent with T4–T5; the antero-labial re-entrant angle LR4 is usually shallow and only rarely deep (Figure 122c'). M^3 is essentially like M^2 but smaller and lacks the antero-labial salient angle BS3. The enamel pattern obliterates with age.

Ellobius is cytologically unique as it has lost the Y chromosome and the *Sry* gene (Vorontsov et al. 1980), and obtained isomorphic XX chromosomes (invariably acrocentric) in both males and females. In male meiosis sex chromosomes behave as if they were heteromorphic (Matveevsky et al. 2016).

Ellobius talpinus (Pallas, 1770) – Common Mole Vole

Taxonomy. The common mole vole is likely an aggregate of 3 closely related allopatric species (Lebedev et al. 2020): *talpinus* (with *tanaiticus* and *ciscaucasicus*), *rufescens* (*transcaspiae* and *kastschenkoi*), and *orientalis*. Two groups can be distinguished based on the morphology of M_3, (Lebedev et al. 2020), the western (*talpinus* and *tanaiticus*) with 3 inner salient angles and with laterally oriented buccal salient angle BS3 (Figure 122a'), and the eastern (*orientalis*) with 2 inner salient angles and caudally oriented BS3 (Figure 122b'). The western taxa (*talpinus* and *rufescens*) are putatively divided by the Volga River (Bakloushinskaya et al. 2019) but the actual border has yet to be resolved.

Distribution (Figure 123)**.** The range (area≈2,593 thousand km^2) is in two major fragments which are ~2,000 km apart. The western fragment lies between the Dnepr River (the western bank is occupied along the lower river-flow) and the Ob' River. To the west of the Volga River, *talpinus* is present up to 48–53° northern latitude in the basins of the Don and Dnepr Rivers. To the east of the Volga River the range encompasses the Bashkortostan, Kurgan, Novosibirsk, Omsk, and Chelyabinsk regions, reaching the 56th parallel. The southern border is on Crimea, on the Caucasus, in north-eastern Iran, northern Afghanistan and north-western Uzbekistan, western, northern and north-central Kazakhstan. The eastern fragment is in the eastern Gobi Desert (Mongolia) and China (Gansu, Nei Mongol, Ningxia, and north-western Shaanxi).

In the forest-steppe and steppe zones, mole voles occupy gently sloping ravines and valleys and sandy floodplains, while preferred habitats in semideserts and northern deserts are loamy and sandy loam soils with abundant geophytes (Popov 1960, Khodasheva 1953). Xeric grasslands and semideserts with sparse perennial vegetation are the principal habitat in Nei Mongol; mole voles occupy sandy, clay and alkaline substrate and colonise irrigated meadows and crops (Xu 2016).

Characteristics. The smaller species of *Ellobius*. Colouration varies from light pinkish-buff dorsally and light-grey ventrally, to all-black (see under subspecies). Skull shows no peculiarities (Figure 121); zygomatic arches are well-expanded (ZgW/CbL=0.68–0.79). The M^3 is short (length=0.93–1.50 mm) and relatively wide (width=1.0–1.3 mm; data are for Chelyabinsk, Russia; Borodin 2009); length of M^3/length of M^2=0.33–0.67 (Topachevskiy 1965). M^3 is of simple shape, in adults usually consisting of the anterior and posterior cusps; the antero-labial triangle T2 is usually blunt or obliterated; it is rarely prominent (Figure 122). Karyotype consists of acrocentric chromosomes: 2n=NF=54 (Vorontsov et al. 1969, Bakloushinskaya et al. 2012).

Variation and subspecies. 4 subspecies are usually recognised based on colouration (Gromov & Erbajeva 1995, Shenbrot & Krasnov 2005); *orientalis* has been moved from *tancrei* to *talpinus* s.lat. following Lebedev et al. (2020).

Ellobius talpinus talpinus (Pallas, 1770)

Mus talpinus Pallas, 1770:568. Type locality: "auſtralioribus Ruſſiae, ad occidentem Volgae ſitis",

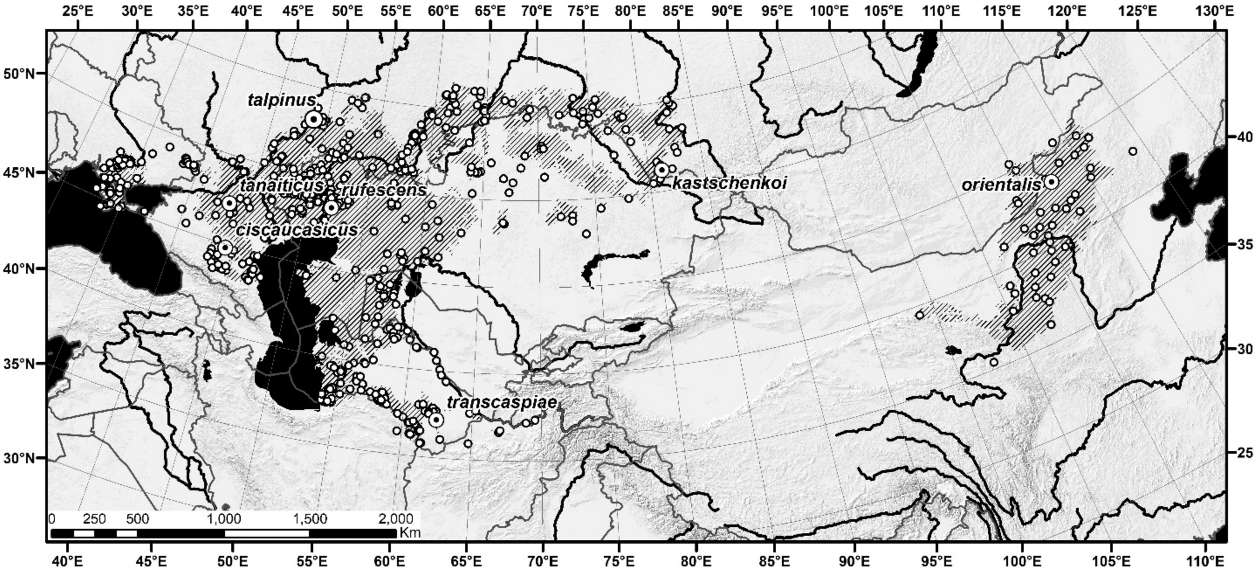


Figure 123: Distributional range of the common mole vole *Ellobius talpinus*.

subsequently restricted to "Kostytschi on the west bank of the Volga between Samara and Syszran [Syzran]" (Chaworth-Musters 1937:158). The exact locality where Pallas saw mole voles in May 1769 ("Am halben Wege nach Koſtytſchi"; Pallas 1771:164) is "half way between Samara and st[anica; i.e. a Cossac village] Kostych, Samarskaya Luka, towards Syzran" (Ognev 1950:682), Russian Federation.

Synonyms. *Spalax minor* Erxleben, 1777 [new name for *talpinus* Pallas]; *Ellobius talpinus ciscaucasicus* Sviridenko, 1936 [nomen nudum]; *Ellobius talpinus tanaiticus* Zubko.
Taxonomy. Possibly a descendant of *E. talpinus palaeoucrainicus* Rekovets, 1985 (Late Pleistocene in Southern Ukraine; Rekovets 1985).

Distribution. West of the Volga River in Ukraine and southern European Russia (including North Caucasus and Crimea). Habitat degradation during the 20th century caused population fragmentation and decline.

Characteristics. Smaller than *kastschenkoi:* H&B=94–121 mm, TL=6–15 mm, HF=18–22 mm, CbL=26.0–29.4 mm, ZgW=19.1–21.8 mm, MxT=6.7–8.0 mm. Pelage is lighter with a reduced amount of contrast between the drab back and the darker head which is poorly lit with blackish-brown hairs; belly is greyish or whitish. The pelage is never black. M_3 with 3 inner salient angles and with laterally oriented BS3.

Ellobius talpinus rufescens (Eversmann, 1870)

G[eorychus] rufescens Eversmann, 1840:175. Type locality: "southern steppes on this [western] side of River Ural"; restricted to "Indersk, Kinderman" (Ognev 1950:685); note that Kinderman (Kindermann in Baranova & Gromov 2003:50) is the name of a collector and not the toponym. The restricted type locality is therefore Indersk, Atyrau Province, north-western Kazakhstan.

Distribution. Western Kazakhstan between the Ural and Emba Rivers.

Characteristics. Dimensions: BWt=32–54 g, H&B=98–133 mm, TL=5–13 mm, HF=19–22 mm, CbL=27.3–29.8 mm, ZgW=19.2–21.3 mm, MxT=6.6–7.8 mm. Colouration is variable; back is usually cinnamon-buff to pinkish-cinnamon, lighter on the flanks and light fawn on the underside; top of the head is dark greyish-brown with a pink tint. Less commonly, the mole voles are light chestnut-brown, more rusty on flanks; the belly is drab and head is brownish-black. The head is not much darker than the rest of the body. Black individuals are rare. M_3 as in the nominal subspecies.

Ellobius talpinus kashtchenkoi Thomas, 1912

Ellobius kashtchenkoi Thomas, 1912b:404. Type locality: "Lokoti [Lokot], 60 kil. [km] west of Smeinogorsk, Tomsk Governorate, Siberia", Zmejnogorskiy Rajon, Altai Krai.

Taxonomy. Until recently reported under the name *talpinus* (see account on the nominotypical subspecies).

Distribution. Northern and western Kazakhstan and Russia; the range is tentatively delimited by the Volga (west) and the Yenisey Rivers (east).

Characteristics. Dimensions: BWt=40–56 g, H&B=104–121 mm, TL=8–13 mm, HF=18–21.5 mm, CbL=26.9–29.5 mm, ZgW=18.0–21.1 mm, MxT=6.2–7.3 mm. Fur colouration is more variable than in any other mole vole, with a monochromatic or 3-coloured pelage (Figure 118a-d). Monochromatic mole-voles are either "brown" or "black". In the former, the back is brown, occasionally shaded drab or wood-brown; the head is dark-brown to black-brown. "Black" individuals (usually referred to as melanistic) are black throughout and occasionally show irregular deep-carmine splotches. Three-coloured mole-voles (classified as transitional) are black (brown-black) from snout to rump, fulvous on flanks and grey below. Among 26 populations studied by Evdokimov & Sineva (2016), 11 contained all three morphs, 6 were dimorphic (5 with "brown" and "black" voles, and 1 with "black" and "intermediate") and the remaining 9 were monomorphic (2 were all-"black", 3 were "intermediate", and 4 were "brown"). Mole-voles are usually "brown" in the steppe zone and polychromatic in the forest-steppe zone. Variation over time was demonstrated in the Kurgan Oblast (the Ural Mts.) where the "black" mole voles increased from

39.5% in 1985 to 58.7% in 1999, while the "brown" morph declined from 44.8% (1985) to 22.4% (1999); the remaining mole voles were intermediate (Evdokimov et al. 2017). In Kuvandykskaya (southern Urals), mole voles were "brown" in 1974–1976, trichromatic in 2001, and dichromatic ("brown" and intermediate) in 2002 (Evdokimov & Sineva 2016). Body mass ($\bar{x}$±SD) varied among 10 local samples from the South Urals from 44.25±0.84 g to 49.73±1.12 g in males, and from 46.85±0.81 g to 57.44±2.02 g in females (Evdokimov & Pozmogova 1992). M_3 as in the nominotypical subspecies (Figure 122a').

Ellobius talpinus transcaspiae Thomas, 1912

Ellobius talpinus transcaspiae Thomas, 1912b:405. Type locality: "Sultan Bent", near Ashgabad, Turkmenistan.

Distribution. Turkmenistan, north-eastern Iran, northern Afghanistan, western Uzbekistan, and south-western Kazakhstan (Mangystau and the vicinity of Aral).

Characteristics. Dimensions: BWt=24–56g, H&B=84–115 mm, TL=8–21 mm, HF=18–23 mm, CbL=23.5–29.5 mm, ZgW=17.2–21.5 mm, MxT=6.0–7.5 mm. Pelage is light: dorsal fur is light pinkish-buff, sides and belly are light-grey and demarcation is distinct. Postero-dorsal head (parietal and occipital regions) is brown, while the frontal and nasal regions are dark brown, taking on a blackish hue towards the nose tip; the temporal region is grey-brown. Hair bases are neutral-grey (back) to light neutral-grey (flanks and belly). M_3 as in the nominal subspecies.

Ellobius talpinus orientalis G. M. Allen, 1924

Ellobius orientalis G. M. Allen 1924:12. Type locality: "Iren Dabasu, eastern Mongolia".

Taxonomy. Status follows Lebedev et al. (2020); is possibly deserving of the status of a species in its own right. Identity of larger and darker mole voles from Nangxia and Gansu is uncertain; Chinese authors (Wang 2003, Xu 2016) classify them as *larvatus* (which is part of *tancrei*).

Distribution. The majority of the range is in central Nei Mongol and the Ordos Plateau (Ningxia, north-western Shaanxi, and Gansu) in China; also marginally the east Gobi Desert in Mongolia (provinces of Dornogovi and Sühbaatar).

Characteristics. Dimensions: H&B=95–108 mm, TL=8–10 mm, HF=19–21 mm, CbL=26.5–27.1 mm, ZgW=18.9–19.0 mm, MxT=6.4–6.5 mm. The smallest subspecies with a bright cinnamon back and an ill-defined facial mark. Pelage is short (loose and fluffy in other subspecies). Cheeks, dorsal side and tail are uniform clear pinkish cinnamon; flanks and underside are dull white. The muzzle and frontal region are fuscous; a tuft of white hair is present near the ear. Hair bases are slate; feet are whitish or silvery. M_3 with 2 inner salient angles and caudally oriented BS3 (Figure 122b').

Ellobius tancrei W. Blasius, 1884 – Eastern Mole Vole

Taxonomy. The eastern mole vole is likely an aggregate of 3 closely related species (Lebedev et al. 2020): *tancrei* (with *albicaudus, larvatus*, and *ursulus), ognevi (coenosus, fuscipes*), and *alaicus*; alaicus and ognevi are in a sister position. Due to unresolved borders we rank these taxa as subspecies.

Distribution (Figure 124). Range covers ~1,702 thousand km^2 in Uzbekistan, Turkmenistan (east of Amu-Darya River), Tajikistan, Kyrgyzstan, southern, eastern and south-central Kazakhstan, margins of Russian Tuva, western and central Mongolia (Arhangay, Bayanhongor, Bayan-Ölgiy, Bulgan, Dundgovi, Dzavhan, Govi-Altai, Govi-Sümber, Hovd, Hövsgöl, Ömnögovi, Övörhangay, Tov, and Uvs) and north-western China (Xinjiang). The western border is on the Amu Darya River and there are few records situated on the right bank (Yakimenko 1984). From the Amu Darya River, the range expends eastwards in a ~750 km wide belt as far as central Mongolia. Mole voles tolerate a wide range of open habitats in the forest-steppes, steppes, semi-deserts and true deserts. They even dwell on rocky substrate with a thin soil layer, on saline soils and fixed sands but are absent from moving sands (Yudin et al. 1979, Sokolov & Orlov 1980). In the mountains mole voles go up to 2,400–3,600 m, depending on the mountain region (Davydov 1988).

Characteristics. Externally and cranially similar to *talpinus* although larger and lighter. Back is light sandy to deep brown and the underside is whitish, occasionally shaded grey or buff; the top of the head is cinnamon to brownish-black and usually contrasts the dorsal fur. Fur is 7.5–9 mm long and soft. Skull shows no peculiarities (Figure 121); zygomatic arches are usually well-expanded (ZgW/CbL=0.67–0.80). There is a great deal of individual and geographic variation in the colouration, size and skull proportions (see under subspecies). In comparison with *talpinus*, the M^3 is longer and relatively narrower with a more complex posterior part (Figure 122c,d). The postero-lingual salient angle T3 is more prominent and the heel is longer, hence M^3 is longer relative to M^2 (length of M^3/length of M^2=0.67–1.00; Topachevskiy 1965). Karyotype differs from *talpinus* in having 1 submetacentric autosomal pair (NF=56), presumably resulting from a pericentric inversion (Bakloushinskaya et al. 2012). In the widespread 2n=54 cytotype the remaining chromosomes are acrocentric. In the remaining chromosomal races, Rb fusions increased the number of bi-armed elements and reduced the 2n to 30–53. The lowest 2n (30) consists of 12 bi-armed and 1 acrocentric pair of autosomes. Cytotypes sharing identical 2n may have different sets of Rb metacentrics. The heterosomes are acrocentric XX in both sexes (Bakloshinskaya et al. 2019).

Variation and subspecies. A polytypic species with 6 subspecies (Gromov et al. 1963, Luo et al. 2000, Wang 2003, Shenbrot & Krasnov 2005, Lunde 2008). Diploid number is stable (2n=54) throughout the majority of the range except in the Pamiro-Alay region where it shows enormous variability (2n=30–54; Bakloushinskaya et al. 2019).

Ellobius tancrei tancrei W. Blasius, 1884

Ellobius tancrëi W. Blasius, 1884:198. Syntypes were obtained "close to Lake Saisan [Zaysan], between Saisan-Posts, in the Altai Mts. (South Siberia)" and in "Kenterlik, Tarbachatai [Tarbagatai] Mts." The type locality was subsequently restricted (Ognev 1950:694) to the "neighbours of Kenderlyk [Kendyrlik; also Przheval'skoe], north of Zaysan, south-east of the Lake Zasan-Nor", Kazakhstan.

Distribution. Zaysan District, Tarbagatai Mts., and Altai Mts. in the East Kazakhstan Region, northern Xinjiang (China), and western Mongolia.

Characteristics. Dimensions: BWt=34.5–82 g, H&B=100–130 mm, TL=7–15 mm, HF=17–26 mm, CbL=25.5–35.3 mm, ZgW=19.0–23.6 mm, MxT=6.4–

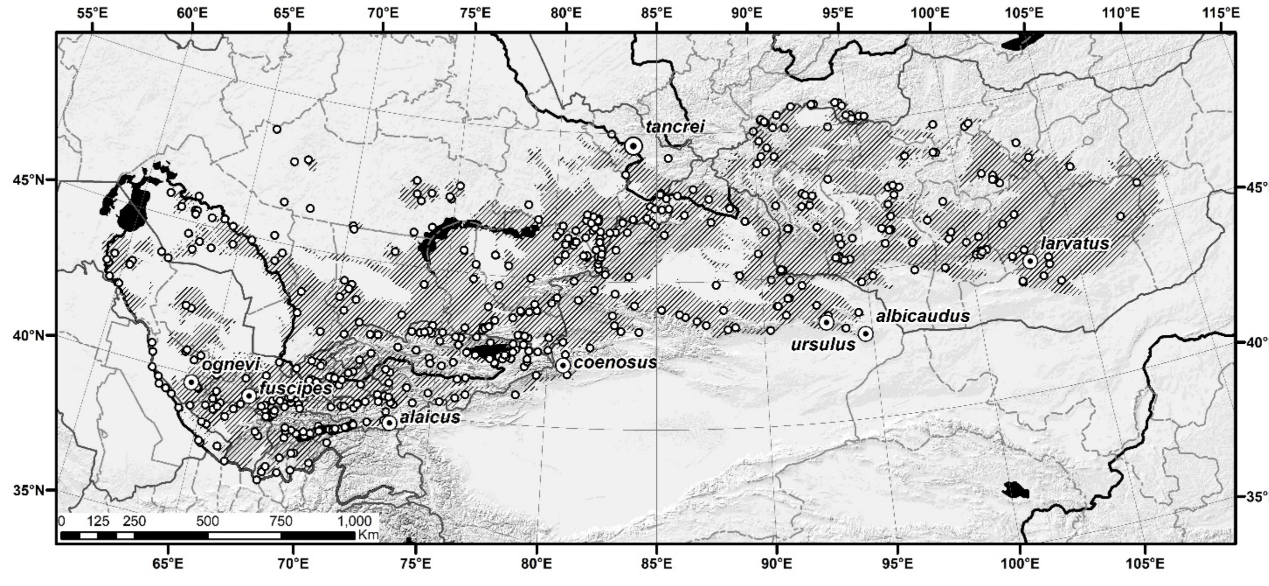


Figure 124: Distributional range of the eastern mole vole *Ellobius tancrei*.

8.5 mm. Dorsal pelage is grey-fawn, occasionally with buffy or light-pinkish tint; reddish hue is rare. Flanks are light sandy and the underside is whitish. Top of head from the nasal to the occipital region is brown-grey to dark mouse-grey. Zygomatic arches moderately expanded (ZgW/CbL=0.71).

Ellobius tancrei fuscipes Thomas, 1909

Ellobius fusciceps Thomas, 1909c:265. Type locality: "Samarkand [Samarquand]. 2000' [610 m]", Uzbekistan.

Synonyms. *Ellobius talpinus ognevi* Dukelskaya, 1927.

Taxonomy. Mardonova et al. (2021) reinstalled *ognevi* as a subspecies in its own right.

Distribution. Uzbekistan (except Fergana) and Tajikistan; marginally in Turkmenistan and Kazakhstan. Occupies sandy-loam and sandy-gravel soils and avoids sands.

Characteristics. Size small: BWt=34–45 g, H&B=97–115 mm, TL=5–20 mm, HF=18–22.8 mm, CbL=25.0–31.0 mm, ZgW=19.7–22.3 mm, MxT=7.0–7.9 mm. Light grey back is shaded nimble cinnamon-buff; flanks are whitish-grey and the underside is whitish, occasionally buffy. The nasal and frontal regions are dark brown; the parietal and occipital parts are more intense cinnamon-buff. Zygomatic arches widely expanded (ZgW/CbL=0.72–0.80). Rostrum is broad and short, braincase smooth and lightly ridged, lambdoidal crest well-marked; M^3 is complex (Figure 122c).

Ellobius tancrei albicatus Thomas, 1912

Ellobius albicatus Thomas, 1912b:401. Type locality: "S.E. [south-east of] Hami Mts., N.E. [north-eastern] Chinese Turkestan. 6000' [1,280 m]", northern Xinjiang, China.

Distribution. Restricted to the Hami region at the extreme eastern end of the Tien Shan Mts., Xinjiang, China (Luo et al. 2000).

Characteristics. A large subspecies; dimensions of the type: H&B=100–130 mm, CbL=27.3–37.6 mm. Hair fine and soft, up to 7.8 mm long on the back, a comparatively narrow buffy to beige dorsal stripe is clearly demarcated from whitish flanks, the line of demarcation set high-up on the sides; ventral fur is whitish; head is contrastingly dark brown; tail covered with blackish hair. Zygomatic arches moderately expanded (ZgW/CbL=0.73).

Ellobius tancrei coenosus Thomas, 1912

Ellobius cœnosus Thomas, 1912b:402. Type locality: "Muzart Valley, Tian Shan ["Chinese Tianshan" (Ellerman & Morrison-Scott 1951:657)], 8000' [2,440 m]," Xinjiang, China.

Synonyms. *Ellobius fusciceps ursulus* Thomas, 1912.

Distribution. Fergana (Uzbekistan) and Tian Shan Mts. in Kyrgyzstan, southern Kazakhstan and Xinjiang (China). Parapatric with *alaicus* in Kyrgyzstan (Bakloushinskaya et al. 2019).

Characteristics. Size large but smaller than in *albicatus:* BWt=42–91 g, H&B=98–135 mm, TL=6.5–17 mm, HF=19–26 mm, CbL=26.3–36.0 mm, ZgW=20.3–25.1 mm, MxT=6.5–8.5 mm. Mole voles are smaller at low altitudes ($\bar{x}$ BWt=46.2 g in Trans-Ili Alatau) and large at high elevations (=51.3 g; Sludskiy et al. 1978). Dorsal hair is ~8 mm long. Upper pelage is deep buffy or brown, ventral side slate or dull white with pinkish buffy shades; facial darkening is moderate, occasionally extending onto the neck. Zygomatic arches moderately expanded (ZgW/CbL=0.70–0.77). Includes the majority of cytotypes with Robertsonian metacentrics.

Ellobius tancrei larvatus G. M. Allen, 1924

Ellobius larvatus G. M. Allen, 1924:11. Type locality: "Artsa, Bogdo, Sain Noin, Mongolia, altitude 6500 feet [1,980 m]"

Distribution. Western and central Mongolia; marginally in Tuva (Russia)

Characteristics. Moderately large subspecies: BWt=38–63 g, H&B=100–125 mm, TL=5–18 mm, HF=19–24 mm, CbL=28.0–33.5 mm, ZgW=19.3–22.4 mm, MxT=6.5–8.3 mm. Pelage is dimorphic, pale or bright (Allen 1940). The former has a light sandy to light drab back, gradually merging into the whitish underside; the nasal and frontal regions of the head are brownish-black, shaded with buff. Feet are white, tail is buffy. In the bright type the back is uniformly pinkish-cinnamon and the head is only slightly darkened on the snout and the frontal region. Hair bases are slate, darker dorsally than ventrally. Pattern of M^3 variable, frequently reduced to two transverse loops.

Ellobius tancrei alaicus Vorontsov, Liapunova, Zakarjan & Ivanov, 1969

Ellobius alaicus Vorontsov, Liapunova, Zakarjan & Ivanov, 1969:127. Type locality: "Southern Kirghizia [Osh Region, Kyrgyzstan], Alay Valley, 3,300 m a.s.l., between [the villages of] Sary-Tash and Bardabo [Bordebe" (p. 129).

Taxonomy. Recognised as a distinct species from karyological evidence; also see the account on *Ellobius.*

Distribution. Restricted to 26,905 km² of the Alay Valley and the adjacent northern slope of Alay Ridge in western and south-western Tien Shan (the Aksay, AtBashi, mid-Naryn, Songkyol', and Tylek valleys). The majority of the range is in southern Kyrgyzstan, reaching the extreme north-eastern Tajikistan; likely marginally present in the adjacent Xinjang (China). Found at altitudes of 1,500–3,600 m a.s.l. Partly overlaps with *coenosus* (cf. Bakloushinskaya et al. 2019).

Characteristics. Moderately large subspecies: BWt=45–67 g, H&B=106–124 mm, TL=8–15 mm, HF=21–23 mm, CbL=29.5–33.5 mm, ZgW=21.2–23.0 mm, MxT=7.2–8.0 mm. Dorsal colour varies from sandy-buff, shaded grey to wood-brown or to intense buff-brown. The flanks are light-grey and the belly is light buffy. The head is wood-brown and does not strongly contrast the back (Figure 118e,f). Cheeks are grey and occasionally shaded buff; lips are black. Feet are covered by silver hairs; the tail is blackish-brown throughout but the terminal hairs of the pencil (length=7.5–12 mm) are light-brown. Juveniles are dorsally blackish grey and lightly shaded brown; flanks and belly are grey to slate. Karyotype: 2n=48, 50, 51, 52, 53, NF=56. Seven variants of karyotypes are known with various combinations of Rb translocations; at least 2 bi-armed autosomal pairs are present (Bakloushinskaya et al. 2019).

GENUS: *Bramus* Pomel, 1892 – Southern Mole Voles

Bramus Pomel, 1892:1159 & 1163. Type species by monotypy: *Bramus barbarous* Pomel (1892:1163). Based on Pleistocene material from "Trara de Nédroma, towards Ain-Mefta", Tunis (p. 1160).

Synonyms. *Afganomys* Topachevsky, 1965.

Taxonomy. A well-defined group of mole voles. The 2 extant species diverged in the Early Pleistocene (>2 Mya; Tesakov 2016). Also see under Bramina.

Distribution. The extant species of *Bramus* occupy the south-western portion of the mole voles' range in eastern Turkey, Armenia, Azerbaijan, Iran, Turkmenistan, Afghanistan, and western Pakistan. The Quaternary range was more extensive. During the Early Pleistocene (Tesakov 2016) or the beginning of the middle Pleistocene (Stoetzel 2013) the lineage of *lutescens* invaded northern Africa from the Middle East via the Libyan-Egyptian route and evolved into 4 endemic species. Mole voles disappeared from northern Africa at the end of the late Pleistocene (Stoetzel 2013).

Characteristics. Externally similar to *Ellobius* s.str. (Figure 118g,h) although larger on average. Both species are sexually dimorphic with larger females. Cranial and dental differences allow for a reliable delimitation between the 2 genera. The sagittal crest is present in *Bramus*, the interparietal is absent in subadults and adults, the posterior end of praemaxillary extends caudally to the naso-frontal suture and the incisive foramina are shorter than M^1. Moreover, the zygoma is set more dorsally (Figure 125). The molar pattern is

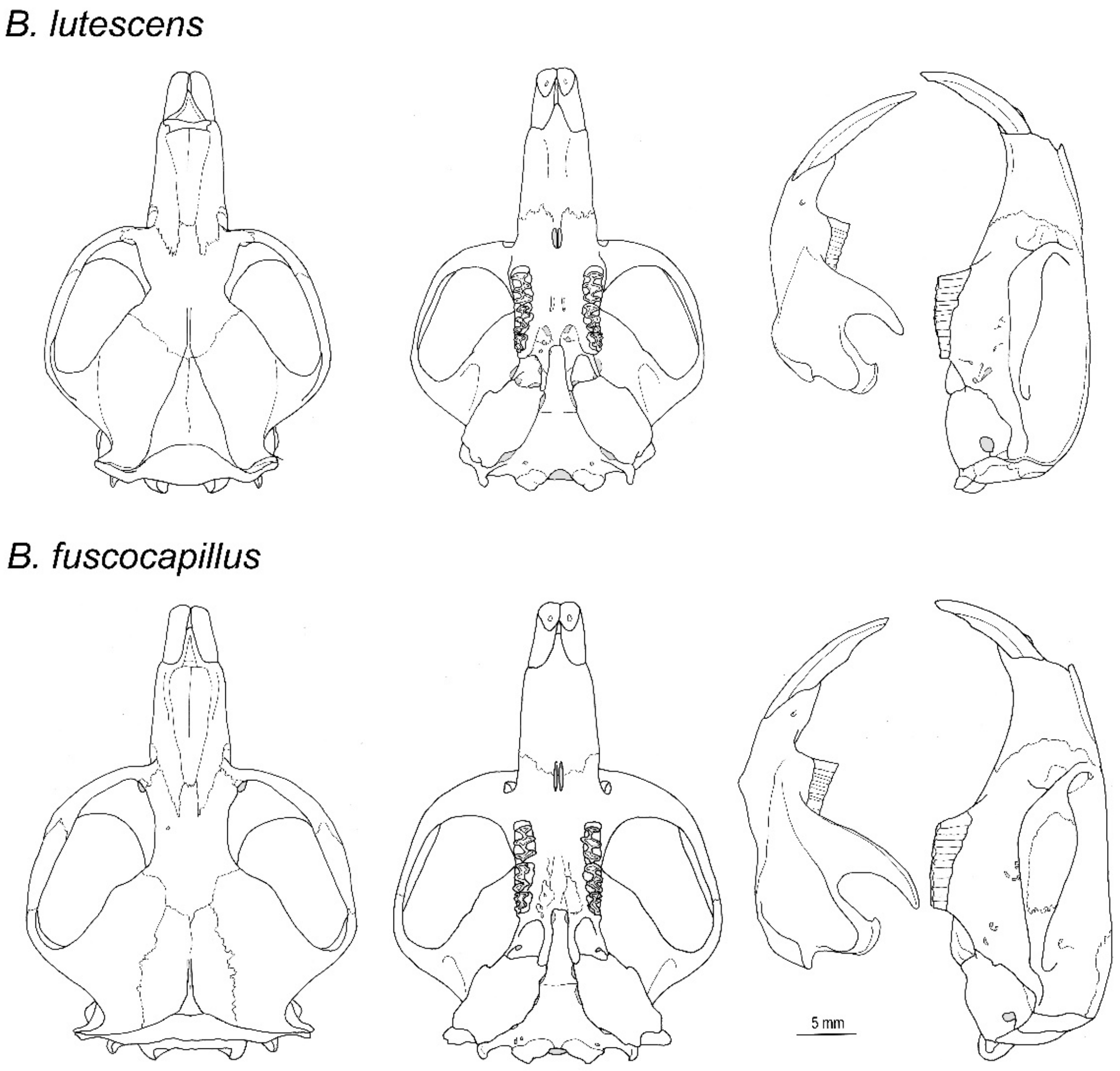


Figure 125: Skull and mandible in southern mole voles (top to bottom): *Bramus lutescens* (Van Province, Turkey) and *B. fuscocapillus* (Karisimir, Afghanistan).

more complex than in *Ellobius*: M^2 contains the same elements as M^1 (including the T1) and has 3 lingual salient angles; M^3 is as complex as in *tancrei* with T4 present. The antero-labial triangle T4 (M_1) is frequently more isolated from the AC (Figure 126). The X-chromosome is submetacentric (Kolomiets et al. 1991).

Bramus fuscocapillus (Blyth, 1843) – Afghan Mole Vole

Georychus fuscocapillus Blyth, 1843:887. Type locality by subsequent designation (Blanford 1881c:118): "Quetta" [Balochistan, Pakistan].

Synonyms. *Ellobius intermedius* Scully, 1887; *Ellobius farsistani* Ugarov, 1928; *Ellobius fuscocapillus legendrei* Goodwin, 1940.

Distribution (Figure 127). The range is an estimated ~294 thousand km^2 and is in 2 main fragments - (i) southern Turkmenistan (Ahal, Balkan, Lebap, and Mary), north-eastern Iran (mainly Golestan, Khorasan-e Janubi, Khorasan-e Rezavi, and Khorasan-e Shemali), and north-western Afghanistan (Fariab and Herat Provinces), and (ii) in eastern Afganistan (Kabul, Paktia, and Vardak) and Pakistani Baluchistan. There are further outliers in Kerman, south-eastern Sistan and Baluchistan (Iran). The Afghan mole vole occupies arid steppes and barren shrubby semi-deserts in low-relief plains, valley bottoms and mountain slopes from sea level to 3,260 m a.s.l.; moving sands and very steep rocky slopes are avoided.

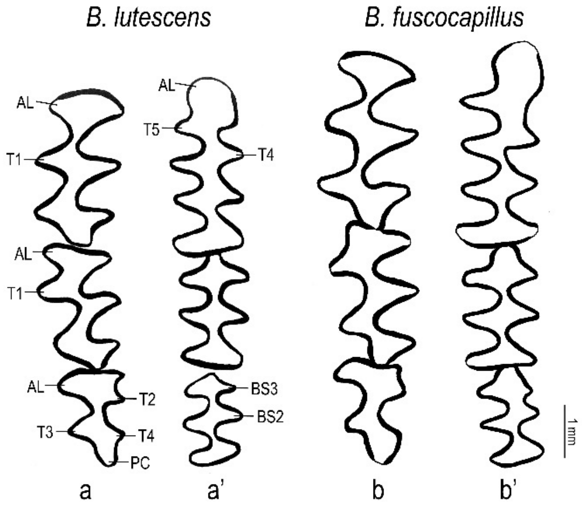


Figure 126: Grinding pattern on upper (a–c) and lower molar rows (a'–c') in southern mole voles *Bramus*: a–*Bramus fuscocapillus* (Karisimir, Afghanistan); b–*B. lutescens* (Van Province, Turkey).

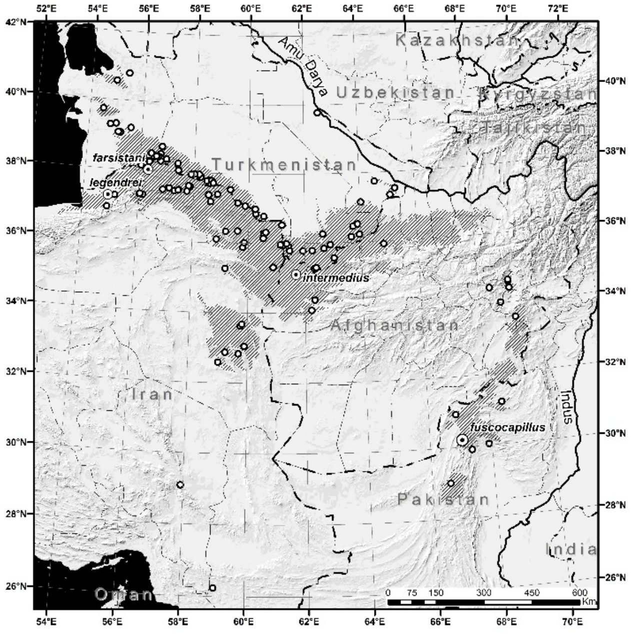


Figure 127: Distributional range of the Afghan mole vole *Bramus fuscocapilus*.

Description. The largest species of mole voles: BWt=20–112 g, H&B=115–160 mm, TL=6–15 mm, HF=19–24 mm, CbL=29.4–40.2 mm, ZgW=21.6–29.2 mm, MxT=7.6–9.3 mm. Sexually dimorphic; females are heavier than males by 27%. Fur is comparatively short and the colouration is variable but usually light and frequently bright: upper parts are yellow with various shades: sandy, avellaneous, pinkish buff or cinnamon buff; the hue is more intense anteriorly, becoming lighter towards the rump. The top of the head from nose to ears is either deep wood-brown, blackish brown, or greyish-black, often glossy and markedly contrasting the nape and back; cheeks and neck are buffy. Flanks are grey, occasionally shaded buff and distinctly demarcated; underparts are pale greyish-yellow. Hair bases are dark neutral-grey dorsally, light-slate on the belly. Feet and tail are white to buffy white; tail has a long (~12 mm) terminal pencil. Young animals are duller. Skull is large with prominent ridges; the sagittal crest reaches the lambdoid crest (Figure 125). Zygomatic arches are more expanded than in *lutescens* (ZgW/CbL=0.73–0.80). Dentition shows no peculiarities (Figure 126a). Karyotype: 2n=36, NF_a=56; 11 autosomal pairs are bi-armed and the remaining 6 pairs are telocentric. The X is medium-large submetacentric and the Y is small telocentric (Kolomiets et al. 1991, Moradi Gharkheloo & Kivanç 2003). This is the only mole vole having ordinary sex chromosome constitution XY/XX and the *Sry* gene.

Variation and subspecies. Monotypic species.

Bramus lutescens (Thomas, 1897) – Transcaucasian Mole Vole

Ellobius lutescens Thomas, 1897:308. Type locality: "Van, alt. 5000 feet " [=1,524 m], Turkey.

Synonyms. *Ellobius woosnami* Thomas, 1905.

Taxonomy. Synonymised with *fuscocapillus* in the mid-20th century (Kuznetzov 1944 and subsequent authors); re-established as a species in its own right by chromosomal data (Vorontsov et al. 1969).

Distribution. (Figure 128). The range covers 281,012 km² in eastern Turkey (Van, Hakkari, Ağrı, İğdir), adjacent Nakhchivan (Azerbaijan), south-eastern Armenia (Ararat, Vayoc Jor, Erevan, Kotayk', Gegarg'unik') and the mountains of western Iran: Zagros range (as far south as Fars Province), the Kühe-Karkas, Central Alborz, and Talysh Mts. Marginally present in south-eastern Azerbaijan (Talysh) and eastern Iraq (As Sulaymaniyah). The range reached the eastern Black Sea coast in the Late Pleistocene (Baryshnikov & Baranova 1983). Transcaucasian mole vole occupies dry grassy habitats and semi-deserts and is frequent around cultivations and irrigated areas. Altitudinal range is 350–3,100 m a.s.l.

Characteristics. Smaller than *fuscocapillus* but still larger on average than *Ellobius tancrei*: BWt=36.5–85.5 g, H&B=105–135 mm, TL=7–15 mm, HF=20–26 mm, CbL=27.1–33.6 mm, ZgW=20.9–25.4 mm, MxT=6.4–8.2 mm. Secondary sexual dimorphism is less marked than in *fuscocapillus*. Fur is up to 8 mm long, fine and dense, dull slate buff, slightly darker above than below; hair tips are occasionally buff (on back) or white (flanks). Colour transition along the side is gradual. Head and cheeks are darker (deep brown); the nape, shoulders and the anterior back are frequently more heavily shaded buffy-brown than the posterior back. Tail is the same colour as the back with a moderately long (7 mm) tuft. The tail stores adipose tissue and is noticeably swollen (bulbous) in individuals in good bodily condition. The skull is smaller than in *fuscocapillus* and the sagittal crest does not reach the lambdoid crest (Figure 125); zygomatic arches are less expanded (ZgW/CbL=0.69–0.77). Molars show no peculiarities (Figure 126b,b'). Karyotype: 2n=17, NF_a=32; all chromosomes are bi-armed. The Y chromosome has been lost (hence X0) together with the *Sry* gene and both sexes have identical karyotypes (Bakloushinskaya & Matveevsky 2018).

Variation and subspecies. Monotypic species.

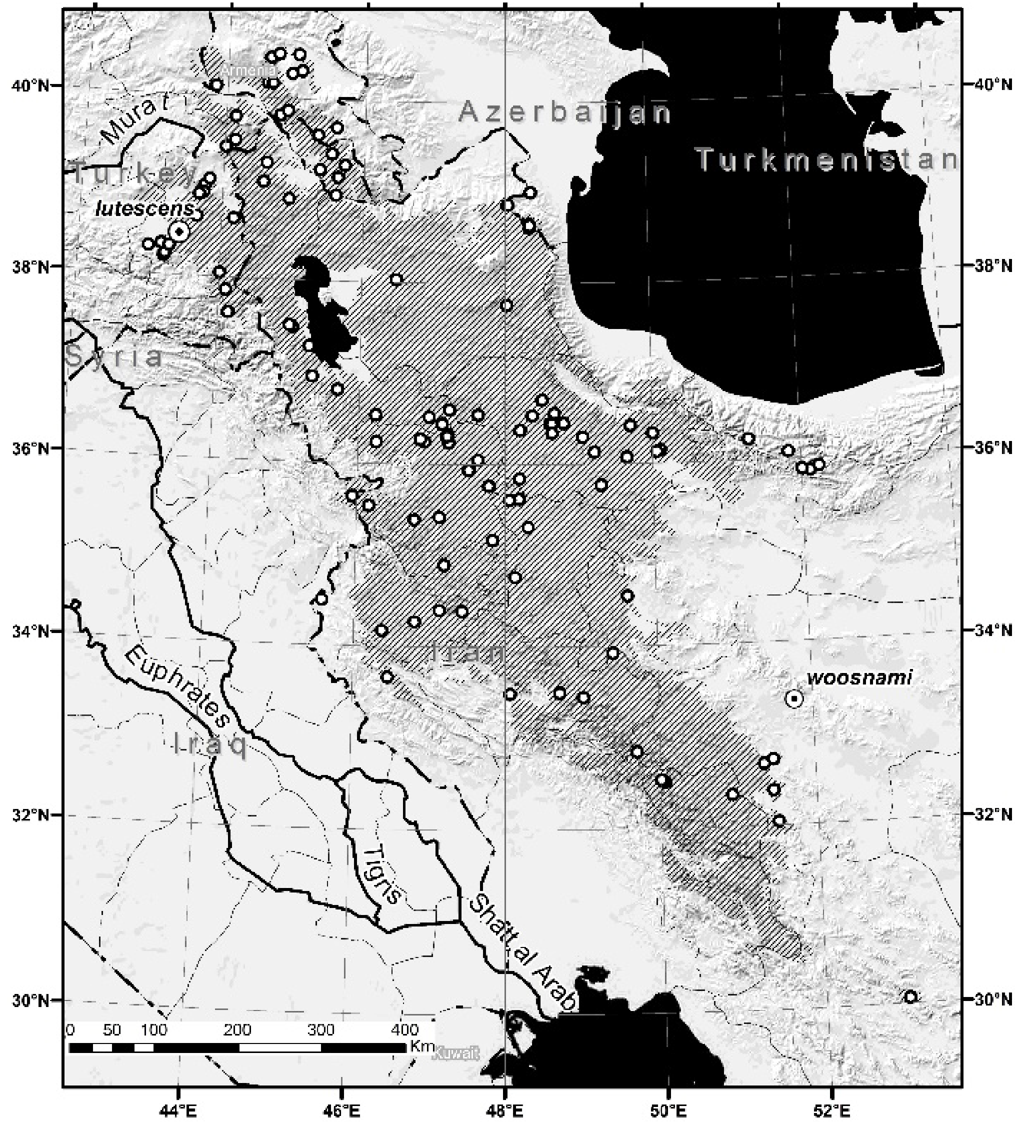


Figure 128: Distributional range of the Transcaucasian mole vole *Bramus lutescens*.

SUBTRIBE:
Pliomyina Kretzoi, 1969

Pliomyini Kretzoi, 1969a:167. Type genus is *Pliomys* Méhely, 1914 (extinct).

Synonyms. Pliomyi Gromov, 1972; Dolomyinae Chaline, 1975.

Taxonomy. Pliomyina contains 3 archaic vole genera with rooted molars, the fossil *Pliomys* and *Dolomys* Nehring, 1898, and the extant *Dinaromys;* some authors (Vasileiadou & Sylvestrou 2022) distinguish between *Propliomys* Kretzoi, 1959, and *Pliomys*. Fossil genera emerged in the Early Pliocene and survived into the Middle Pleistocene (*Dolomys*) and until the end of the Pleistocene (*Pliomys*). When the first Dinaric voles were collected in the early 1920s they were classified as snow voles *Chionomys* (Martino & Martino 1922, Bolkay 1924) but were transferred to *Dolomys* shortly afterwards because of their rooted molars (Hinton 1926a). Kretzoi (1955) split *Dolomys* (which in Hinton's definition also included *Pliomys*) into the current 3 genera relying on molar size, shape of the anterior cap of M_1, and structure of the hard palate. Kretzoi's revision was entirely typological and undervalued variation within-taxa in all the above traits and was not universally accepted. Some authors (e.g. Bartolomei 1969, 1980) continued to treat *Dinaromys* as a synonym of *Dolomys*. Brink (1968) even synonymised the recent species with the Villaniyan *Dolomys milleri* Nehring, 1898, from Eastern Europe which is unlikely. Namely, *D. milleri* retained the *Mimomys*-like islet on the anterior cap of M_1 (cf. Méhely 1914) which is never present in recent *Dinaromys*.

Dinaromys cannot be securely distinguished from *Pliomys* by the morphology of M_1 (our unpublished results) or by the enamel banding pattern (Koenigswald 1980). In the opinion of Chaline et al. (1999), *Dinaromys* "is actually a cement-bearing type of *Pliomys*". Cement is a relatively modern acquisition in *Dinaromys* and fossil species (*allegranzii* and *dalmatinus*) are entirely without. *Dinaromys* appeared in the fossil record during the Villanyian period of the upper Pliocene (Kryštufek & Bužan 2008). If its ancestor was indeed *Pliomys*, as usually hypothesised (Gromov & Polyakov 1977, Chaline et al. 1999), then *Pliomys* is unavoidably paraphyletic with respect to *Dinaromys*. We continue using *Dinaromys* as a genus distinct from *Pliomys* on the basis of convention rather than evidence, pending a revision of the entire tribe.

The position of Pliomyina inside Arvicolinae is still disputed. Hinton (1926b) believed that *Dolomys* is ancestral with respect to the *Mimomys* lineage, a fossil group of voles with rooted molars that gradually evolved into *Arvicola* during the Pleistocene. Chaline & Mein (1979) also regarded *Dinaromys* as a close relative of *Arvicola*. Kretzoi (1955) placed *Dinaromys*, along with *Pliomys* and *Dolomys*, into the Ondatrini; this family-group name is now usually restricted to the Nearctic *Ondatra* and *Neofiber*. In the past *Dinaromys* was classified in Clethrionomyini (Hooper & Hart 1962, Gromov & Polyakov 1977, McKenna & Bell 1997), Dolomyinae (Chaline 1975), Prometheomyini (Pavlinov 2003) or to Pliomyini (Musser & Carleton 2005, Pardiñas et al. 2017). Other studies have suggested a sister position of the extant *Dinaromys* against Bramina (Abramson et al. 2021) or against the Clethrionomyini + Arvicolini combined (Robovsky et al. 2008).

GENUS: *Dinaromys* Kretzoi, 1955 – Dinaric Voles

Dinaromys Kretzoi, 1955: 351. Type species: *Microtus (Chionomys) marakovici* Bolkay (= *bogdanovi* V. Martino & E. Martino).

Taxonomy. The genus is usually considered to be monospecific. *Mt*-phylogenetic reconstruction retrieved three highly divergent allopatric lineages (Northwestern,

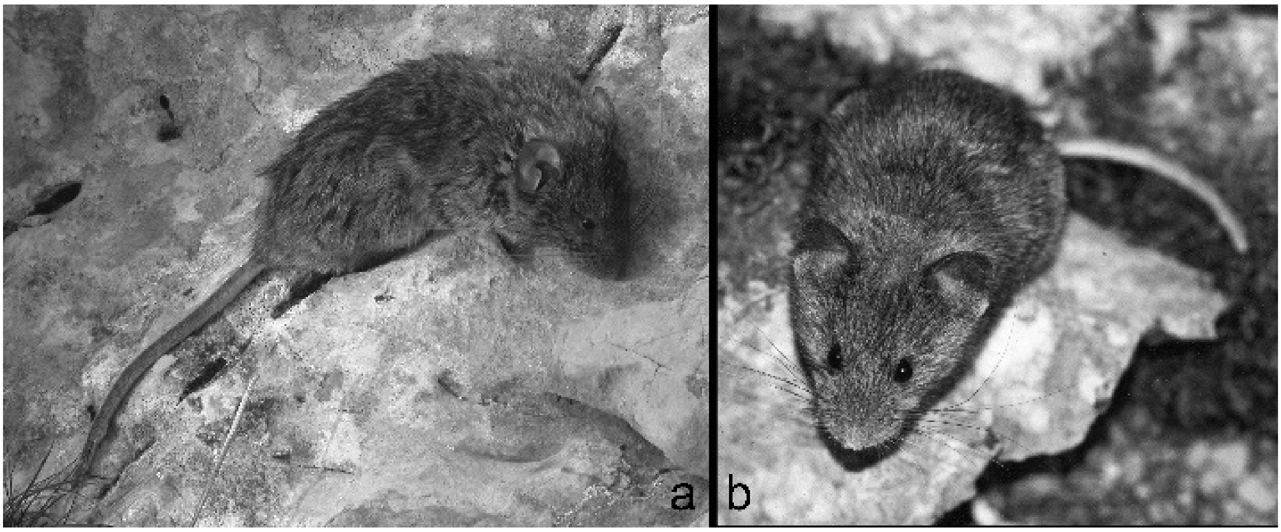


Figure 129: Martino's vole (*Dinaromys bogdanovi*): a–the nominal subspecies from Mt. Bjelašnica, Bosnia and Herzegovina; b–ssp. *gradojevici* from Mt. Bistra, North Macedonia. Photo by Boris Kryštufek (a) and Alenka Kryštufek (b).

Central and Southeastern) delimited by the Neretva and Drim Rivers, respectively. These lineages presumably originated from a gradual southerly expansion with a subsequent allopatry approximately 1 and 0.3 My, respectively. The Northwestern lineage shows the highest divergence from all other samples. (Kryštufek et al. 2007). The major genetic (K2P) distance is indicative of a speciation event and the *Mt*-structuring was supported by microsatellite markers (Buzan et al. 2010a). We therefore classify the two major lineages as distinct species. Earlier studies (Todorović 1956, Gill et al. 1987) stipulated the major divergence further south between North Macedonia and Kosovo. The skull morphology is remarkably invariant throughout the range of the genus, presumably due to the stabilising selection posed by the narrow limits of the adaptive zone of Martino's vole (Kryštufek et al. 2012a).

Distribution. Calcareous mountains along the eastern Adriatic coast, between the northern Mt. Velebit and the Mt. Mala Kapela (Croatia) as far south as Mt. Galičica (North Macedonia). During the Pleistocene the range of the *Dinaromys* also embraced the northern Adriatic region as far west as the Po River. A gradual shrink, putatively the result of competitive exclusion with *Chionomys nivalis*, started as early as the Middle Pleistocene with a significant loss of range in the Early Holocene. Martino's voles are found in underground habitats on limestone bedrock. Preferred habitats are rare and widely scattered but stretch from close to sea level into the alpine zone; altitudinal range is 10–2,200 m however only 17% of localities are from below 1,000 m (Kryštufek & Bužan 2008).

Characteristics. Moderately large voles with a comparatively long tail (TL/H&B=0.58–0.81). Snout is pointed rather than blunt; eyes are moderately large (diameter=3.0–4.6 mm). Ears are large, rounded and protrude above hairs (Figure 129). Mystacial whiskers are among the longest in the subfamily (length=50–65 mm). Feet are long with 5 palmar and 6 plantar pads; claws are rather small but sharp. Fur is soft and long (length=10.5–12 mm); the black-tipped protruding hairs overhang by 1–2.5 mm. The tail is densely clad by stiff white hairs which largely cover the annulation; the terminal pencil measures 2–6 mm. Pelage is light-greyish but takes on light brown shades with advanced age. Fur is grizzled by black-tipped hairs which become denser along the spine. Flanks are greyish with a buff or light-brown shade. The underside is grey with ample white hairs and never has a brownish tint; the demarcation on the flanks is distinct although not sharp. Young are darker grey with a bluish shade. The ears are grey and feet are cream, rarely white. Females have 6 nipples (2 inguinal pairs and a posterior pectoral pair). Glans penis is cylindrical and 1.3–1.6-times longer than wide. Baculum is of trident type with a notch on the posterior margin of the base; ossification of the distal baculum is postponed (cf. Figure 130 c & d) which is likey connected to delayed sexual maturity (Kryštufek et al. 2000).

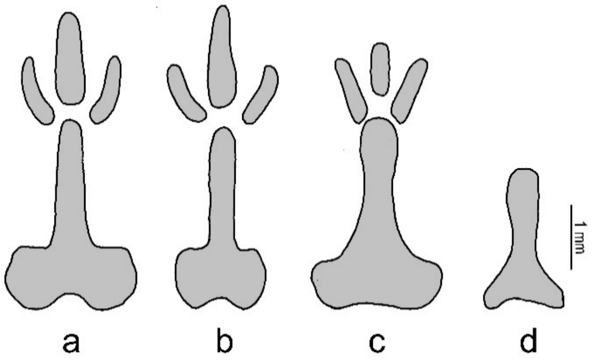


Figure 130: Baculum in Dinaric voles *Dinaromys*; body mass serves as a proxy for age. a–*D. b. bogdanovi* (Mt. Zelengora, Bosnia and Herzegovina; 74 grams); b–*D. b. grebenscikovi* (Mt. Bista, North Macedonia; 66 grams); c,d–*D. longipedis* (Mt. Kozjak, Split, Croatia; 58.5 and 33.5 grams, respectively). Distal baculum is still cartilaginous in inset d.

Skull is large, strongly built and rather narrow (ZgW/CbL=0.53–0.60). Dorsal profile is gently bowed with light concavity in the orbital region. The nasals project to the level of incisors' front surface and the occipital region is truncated in the lateral view. Adult skull is ridged although the temporal ridges fuse into the sagittal crest only in very old animals. The interorbital region is not particularly constricted; postorbital squamosal knobs are well-marked. The auditory bullae are comparatively large and lack internal spongy tissue; their walls are thin. The mastoid portion is only slightly inflated. The posterior palate has a broad and low medial crest and very shallow postero-lateral pits (Figure 10h). Mandible shows no peculiarities; the articular process is long and slender (Figure 131).

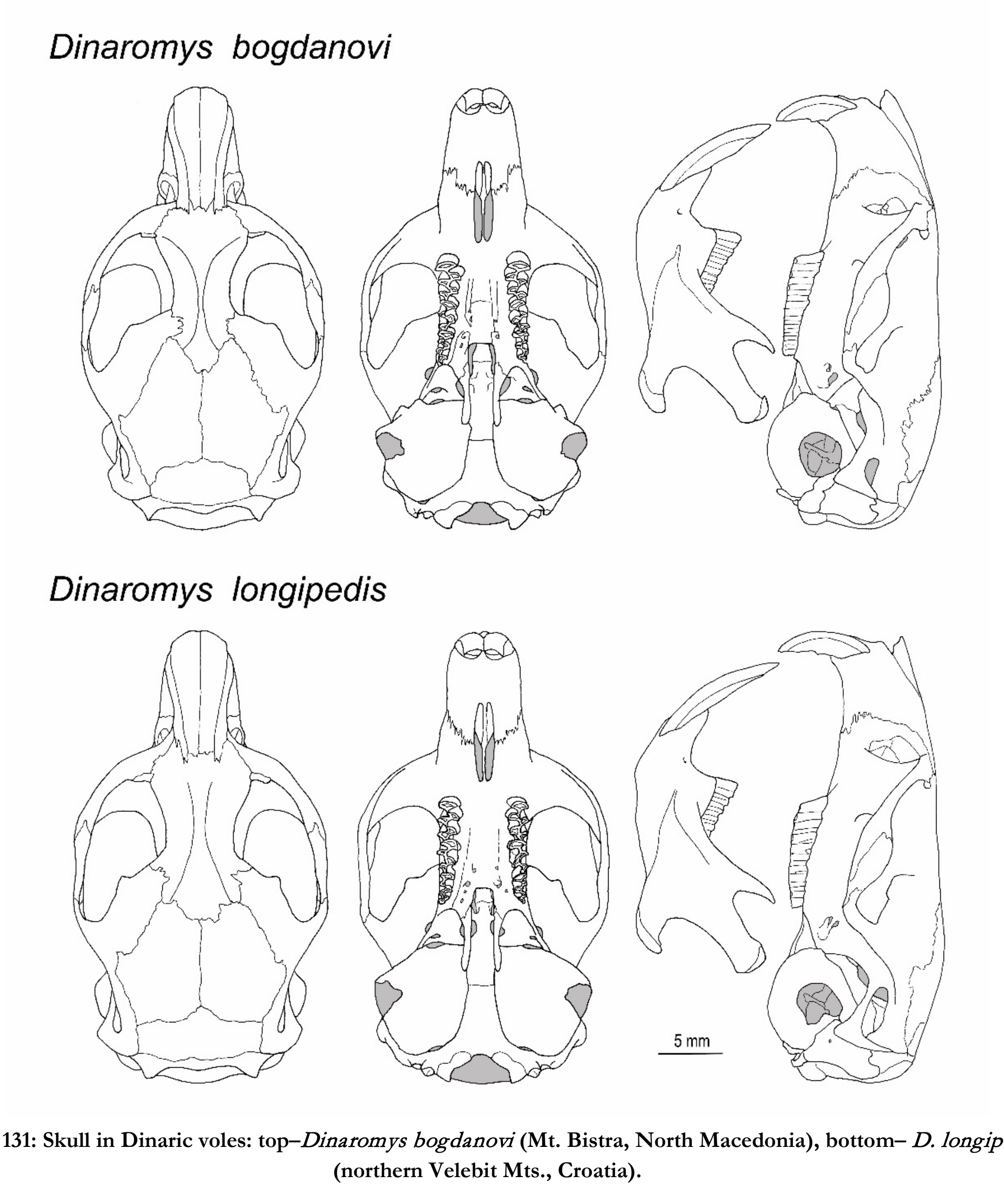


Figure 131: Skull in Dinaric voles: top–*Dinaromys bogdanovi* (Mt. Bistra, North Macedonia), bottom– *D. longipedis* (northern Velebit Mts., Croatia).

The upper incisors are sometimes slightly grooved, particularly in young voles; the lower incisors are deeper than they are wide. The molars are rooted with two roots each. The roots form at 4–6 months of age (Kryštufek et al. 2000), and the molar capsules do not rise up conspicuously in the floor of the orbit, hence not obstructing the sphenorbital fissure (Hinton 1926a). The average growth rate of the M_1 root (0.08 mm/month) is approximately ½ the growth rate in *Clethrionomys glareolus*. Molars show more developed lingual salient angles than buccal angles. M^3 has 3 salient angles on either side; the antero-labial salient loop BS2 is reduced and widely confluent with the anterior loop. M_1 consists of posterior lobe, 5 alternating triangles and the anterior cap with 2 salient angles (LS5 and BS4).

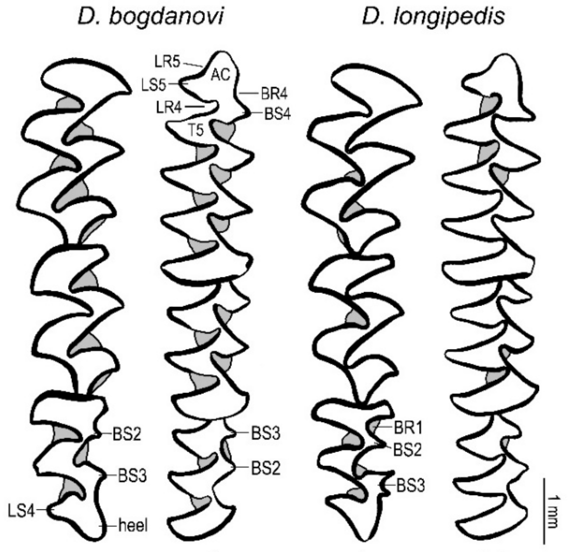


Figure 132: Molar pattern in Dinaric voles. *Dinaromys bogdanovi*: upper (a) and lower (a') row (Mt. Orjen, Montenegro). *Dinaromys longipedis*: upper (b) and lower (b') row (Vrhovine, Mala Kapela, Croatia).

The outer BS4 is semi-isolated in rare cases. The cap is asymmetric largely due to a deep anteriormost re-entrant angle LR4 (Figure 132). Shape depends heavily on age. Juvenile molars show aberrant morphologies which may persist in subadult voles (Figure 133a–h). With advanced age, the anteriormost salient angles (LS5 and BS4) amalgamate with the cap and the re-entrant angles BR4 and LR5 blend (Figure 132i–k). Juvenile molars occasionally have a "balcony" on the base of the posterior loop (Figure 133a,b,f). The enamel is undifferentiated or positively differentiated between the lee and luv sides. Luv enamel is usually 0.08–0.1 mm thick; on the lee side the enamel band narrows rapidly from the apex of the anticline inwards until it disappears at approximately the middle of the triangle. The enamel on the luv side consists of the inner lamellar and the outer radial layer; the lamellar layer extends into the lateral side of the lee side where some primitive tangential enamel is also present (Koenigswald 1980).

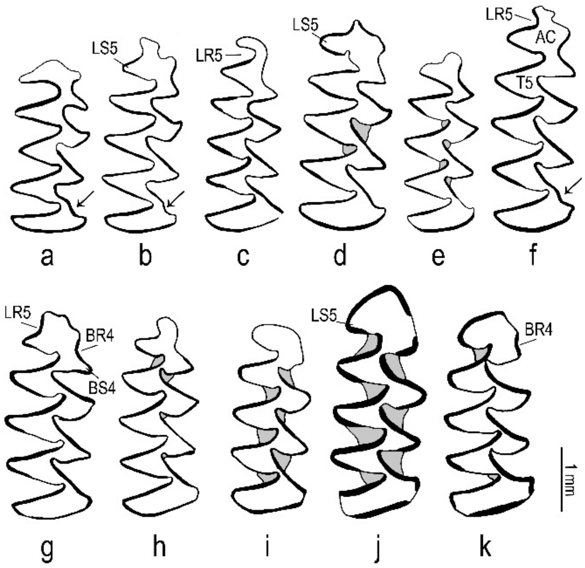


Figure 133: Right first lower molar (M_1) in *Dinaromys longipedis* (i) and *D. bogdanovi* (the rest). Individuals are sorted from the lightest to the heaviest; body mass serves as a proxy for age. Note the great variation in the thickness of the enamel band, deposition of cement and shape of the anterior cap. Arrows point on a "balcony" on the labial side of the posterior loop. a–Mt. Bistra, North Macedonia (23 grams); b–Mt. Zelengora, Bosnia and Herzegovina (25 grams); c–Mt. Komovi, Montenegro (38 grams); d–Mt. Bjelašnica, Bosnia and Herzegovina (41 grams); e–east of Mostar, Bosnia and Herzegovina (43 grams); f, g–Mt. Orjen, Montenegro (48 and 49.5 grams, respectively); h–Mt. Bjelasica, Montenegro (51 grams); i–Malačka above Split, Croatia (58.5 grams); j–Mt. Jablanica, North Macedonia (68 grams); k–Mt. Lovćen, Montenegro (81 grams).

Key to species

1a) Upper side of tail is uniformly dark (Figure 134a); lateral metatarsal pad lies posterior to interdigital pad 1 (Figure 135b); glans penis is short (4.0–4.7 mm); central digit of the distal baculum is the same length or longer as the lateral digit; present in Central Bosnia and east of the Neretva River ……………….................... *bogdanovi*

1b) Upper side of tail is dark anteriorly and white posteriorly (Figure 134b); lateral metatarsal pad lies at the level of interdigital pad 1 (Figure 135c); glans penis is long (4.6–5.6 mm); central digit of the distal baculum is shorter than the lateral digit; present west of the Neretva River ……………………................… *longipedis*

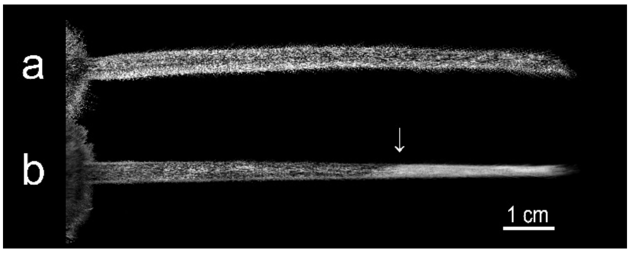


Figure 134: Tail in Martino's voles: *D. bogdanovi* (a–Mt. Bistra, North Macedonia) and *D. longipedis* (b–Poklečani, Bosnia and Herzegovina). Note the white terminal part in *D. longipedis*. Photo by David Kunc.

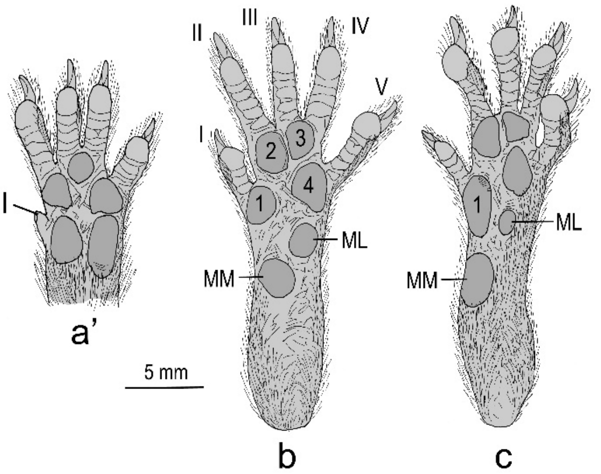


Figure 135: Left palm (a') and sole (b,c) in *Dinaromys bogdanovi* (a'–Mt. Zelengora, Bosnia and Herzegovina; b–Dečani, Serbia) and *D. longipedis* (c–Malačka, Croatia). Digits are indicated using Roman numerals (thumb=I). Metatarsal pads: MM–medial pad, ML–lateral pad.

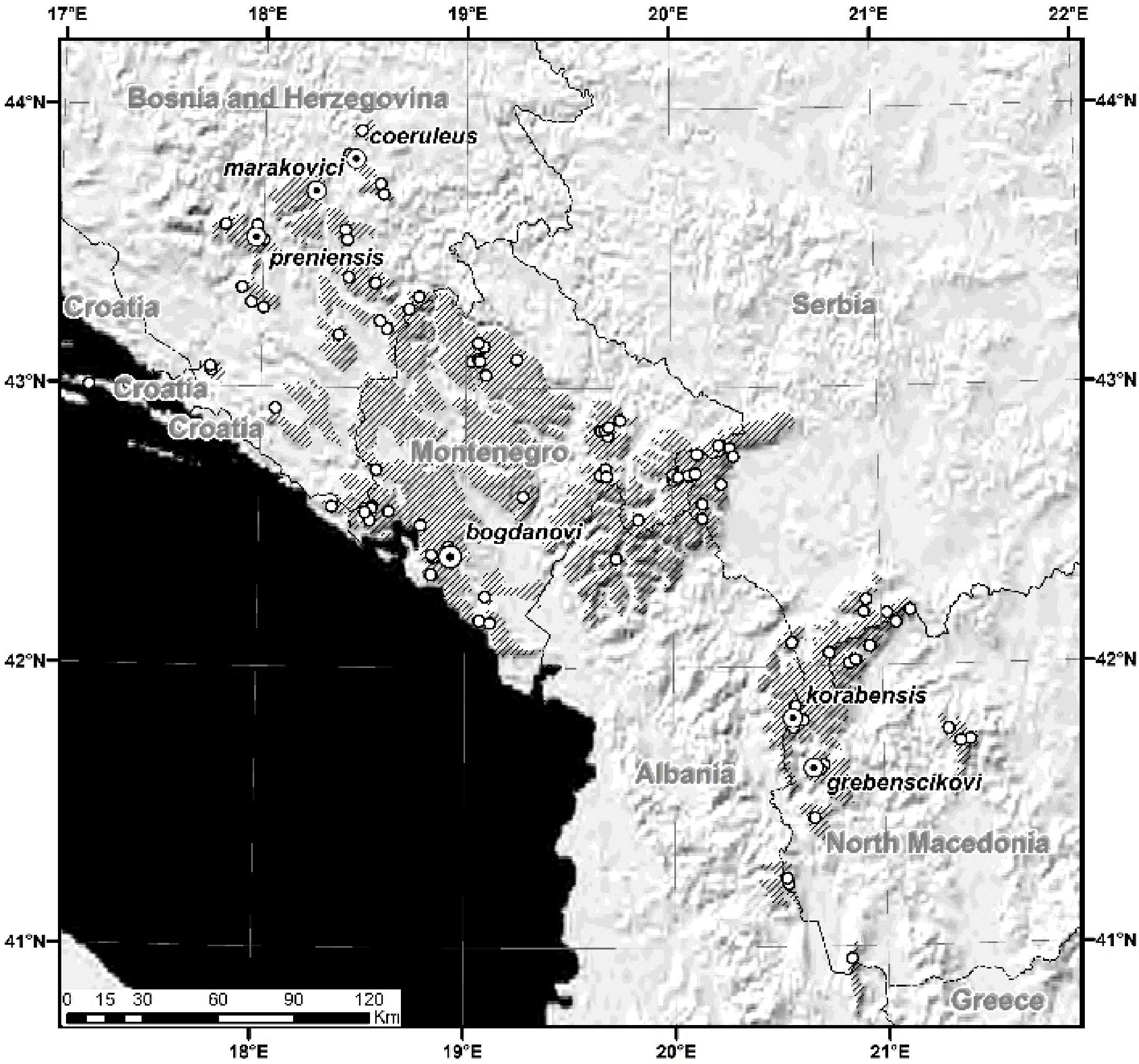


Figure 136: Distributional range of Martino's Dinaric vole *Dinaromys bogdanovi*.

Dinaromys bogdanovi (V. Martino & E. Martino, 1922) – Martino's Dinaric Vole

Distribution (Figure 136). The south-eastern part of the range of *Dinaromys* in the mountains of Central Bosnia and scattered across Herzegovina, throughout the majority of Montenegro, in northern Albania (Prokletije Mts.), marginally in Kosovo, and scattered in western North Macedonia. Two records are known from the Croatian coast (Pelješac Peninsula and Mt. Sniježnica). The range is estimated at 13,705 km^2 and the altitudinal range is from close to sea level (10 m) up to 2,200 m.

Characteristics are as for the genus. Dimensions: BWt=46.5–99 g, H&B=123–158 mm, TL=82–114 mm, HF=23.5–27.7 mm, EL=16.2–21.2 mm, CbL=30.6–35.3 mm, ZgW=17.3–20.5 mm, MxT=7.6–9.0 mm. Tail is uniformly dark on the dorsal side throughout its length (Figure 134a). Lateral metatarsal pad is shifted posterior to interdigital pads 1–4 (Figure 135b). Glans penis is less robust than in *longipedis*; length×width=4.0–4.7×3.0–3.1 mm. Distal baculum is comparatively large and the central digit is longer than the lateral digits (Figure 130a,b). Proximal baculum (length=2.6–2.8 mm) is 1.8–2.8-times longer than the central distal digit; central digit (length=1.1–1.5 mm) is 1.0–1.6-times longer than the lateral digit (length=0.9–1.2 mm). Karyotype (2n=54, NF_a=54) is stable across the range of the species (Zima et al. 1997).

Variation and subspecies. The two phylogeographic lineages (Central and Southeastern; Kryštufek et al. 2007) correspond with the two morphotypes based on the shape of the anterior loop of M_1 (Todorović 1956) being classified as distinct subspecies.

Dinaromys bogdanovi bogdanovi (V. Martino & E. Martino, 1922)

Microtus (Chionomys) bogdanovi V. Martino & E. Martino, 1922:413. Type locality: "Cetinje, Montenegro. Alt[itude] 680 m."

Synonyms. *Microtus (Chionomys) Marakovići* Bolkay, 1924; *Dolomys bogdanovi preniensis* V. Martino & E. Martino, 1940; *Dolomys bogdanovi marakovići* natio *coeruleus* K. Martino, 1948 [valid as *coeruleus* Đulić & Mirić, 1967]; *Dolomys bogdanovi trebevićensis* Gligić, 1959 [nomen nudum].

Taxonomy. Corresponds to the Central phylogeographic lineage. Screening of partial *Cytb* sequences retrieved higher nucleotide diversity than in ssp. *grebenscikovi* (Krystufek et al. 2007).

Distribution. The north-western part of the species range in Bosnia and Herzegovina, Montenegro, northern Albania and north-western Kosovo (Serbia). Altitudinal range is the same as for the species.

Characteristics. Differs from ssp. *grebenscikovi* in the *Cytb*-make-up (Krystufek et al. 2007). The antero-lingual re-entrant angle LR4 is longer (length=0.77–1.50 mm). In comparison with ssp. *grebenscikovi*, the proximal baculum has a wider basal expansion (=1.9–2.3 mm), the central distal baculum is shorter (1.1–1.4 mm) and the lateral digits are longer (1.1–1.2 mm). Dimensions: BWt=46.5–99 g, H&B=123–158 mm, TL=82–114 mm, HF=23.5–27.7 mm, EL=16.2–21.2 mm, CbL=30.6–35.3 mm, ZgW=17.3–20.5 mm, MxT=7.6–9.0 mm.

Dinaromys bogdanovi grebenscikovi (V. Martino, 1934)

Dolomys grebenščikovi V. Martino, 1934:84. Type locality: "Senečki suvati. Bistra Mountains Alt[itude] 2000m", North Macedonia.

Synonyms. *Dolomys grebenščikovi korabensis* V. Martino & E. Martino, 1937.

Taxonomy and nomenclature. Corresponds to the South-eastern phylogeographic lineage. Screening of partial *Cytb* sequences retrieved a recent population expansion and lower nucleotide diversity than in the nominal subspecies (Krystufek et al. 2007).

The year *grebenscikovi* was first published is quoted either as 1934 or 1935. The reprint of Martino's paper has 1934 on the front cover and Mirić (1962:176) explicitly quoted 1934 as the correct year of naming *grebenscikovi;* this was accepted in Đulić & Mirić (1967:19) and Niethammer & Krapp (1982:199). Ellerman & Morrison-Scott (1951:675) quoted 1935 which was subsequently followed by many authors.

Distribution. The south-eastern part of the species range in south-western Kosovo (Serbia) and North Macedonia. Almost certainly present in north-eastern Albania. Altitudinal range is 1,500–2,200 m.

Characteristics. Differs from the nominal subspecies in *Cytb*-sequences (Krystufek et al. 2007). The mesial portion of the antero-lingual re-entrant angle LR4 is shorter (length=0.71–0.94 mm). In comparison with ssp. *bogdanovi*, the proximal baculum has a narrower basal expansion (=1.4–1.7 mm), the central distal baculum is longer (1.4–1.5 mm) and the lateral digits are shorter (0.9–1.0 mm). Dimensions: BWt=46.5–89 g, H&B=124–153 mm, TL=80–100 mm, HF=23.3–27.1 mm, EL=16.1–21.0 mm, CbL=31.1–34.3 mm, ZgW=17.1–19.5 mm, MxT=7.7–9.3 mm.

Dinaromys longipedis (Đulić & Vidinić, 1967) – Western Dinaric Vole

Dolomys bogdanovi longipedis Đulić & Vidinić, 1967:163. Type locality: "Rupe-Kolibe Petra Četnika, Čatrna voda, [Mt.] Dinara, 1420 m above sea level, Dalmatia, Yugoslavia", now Croatia.

Taxonomy. Phylogenetically older than *bogdanovi*, with a higher nucleotide diversity (Krystufek et al. 2007).

Distribution (Figure 137). The north-western part of the range of the genus to the west of the Neretva River in Croatia and western Bosnia and Herzegovina. The area of *longipedis* is small (5,735 km^2) and fragmented. The altitudinal range as in *bogdanovi* (20–2,100 m) but the majority of known sites are <1,500 m a.s.l. (Kryštufek & Bužan 2008).

Characteristics. Dimensions: BWt=49–84 g, H&B=130–154 mm, TL=92–110 mm, HF=23.0–28.2 mm, EL=12.4–20.0 mm, CbL=30.5–34.8 mm, ZgW=17.3–19.5 mm, MxT=7.7–8.6 mm. The terminal

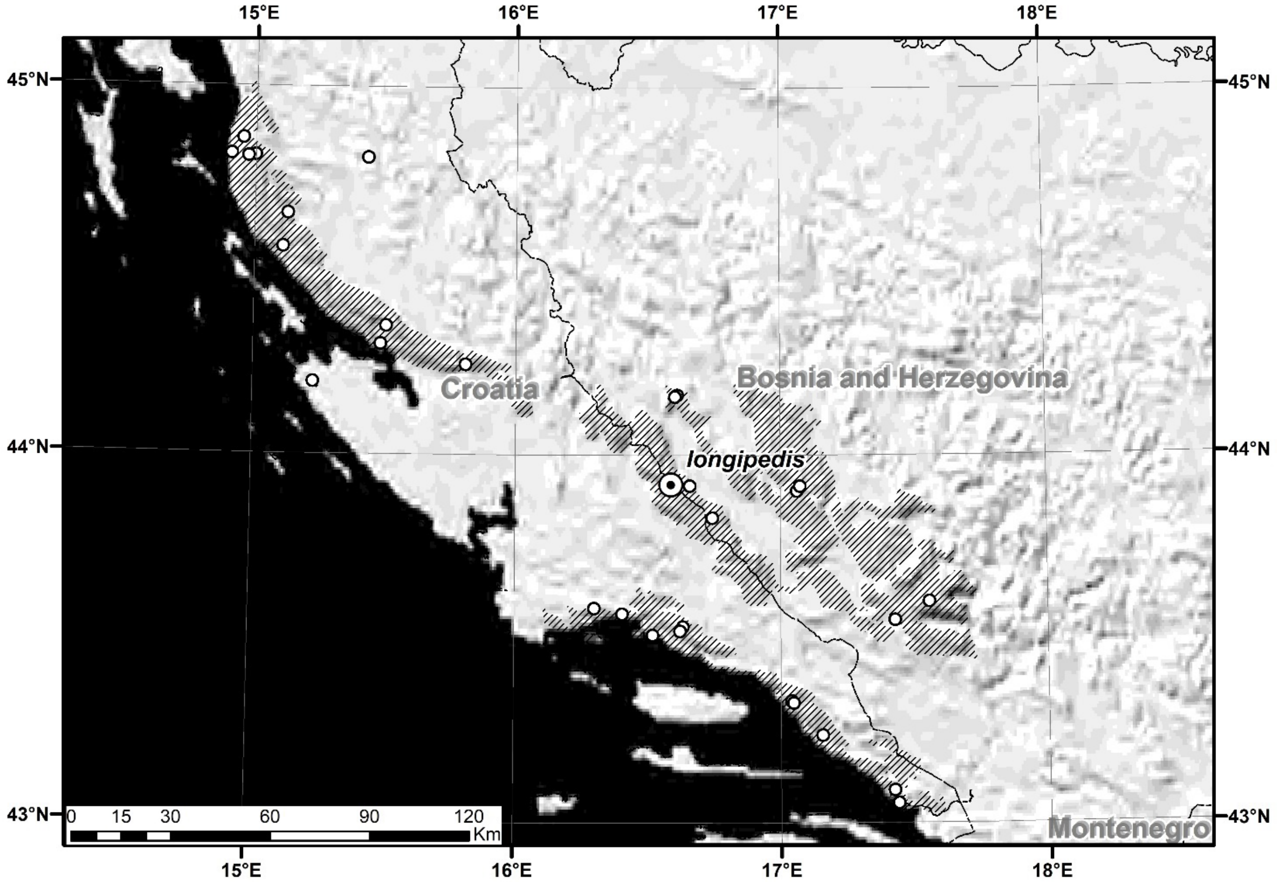


Figure 137: Distributional range of the western Dinaric vole *Dinaromys longipedis*.

5–35% (usually 10–20%) of the tail is white, contrasting the proximal section which is dark on its upper side (Figure 134b). Lateral metatarsal pad lies at the level of interdigital pad 1 (Figure 135 c). Glans penis is more robust than in *bogdanovi*; length×width=4.6–5.6×3.7–4.2 mm. Proximal baculum (length×width=2.8–3.0×2.1–2.2 mm) is 2.7–4.2-times longer than the central distal digit; central digit (length=0.7–1.1 mm) is 0.6–0.9-times shorter than the lateral digit (length=1.1–1.3 mm) (Figure 130c). Karyotype is not known.

Variation and subspecies. The minimum spanning network, based on partial *Cytb*-gene showed a deep gene tree with broadly sympatric albeit highly divergent haplotypes, therefore suggesting a secondary admixture of allopatrically evolved populations (Kryštufek et al. 2007). The species is regarded as monotypic due to its lack of obvious geographic pattern.

SUBTRIBE:
Lagurina Kretzoi, 1955

Lagurini Kretzoi, 1955:353. Type genus is *Lagurus* Gloger.

Taxonomy. Early authors regarded lagurines as being closely related to lemmings (Schreber 1792, Fischer 1814, Gloger 1841); e.g. Brants (1827) classified them into *Lemmus*, and Murray (1866) into *Myodes*. Miller (1896) showed that lagurines are voles (Microti) and not lemmings (Lemmi), and classified *Lagurus* as a subgenus of *Microtus*; Hinton (1926a) elevated *Lagurus* to a generic rank. Subsequent authors classified lagurines either as a subfamily (Lagurinae; Koenigswald & Martin 1984), a tribe (Lagurini; Gromov & Baranova 1981, Shenbrot & Krasnov 2005, Robovský et al. 2008, Pardiñas et al. 2017), or a subtribe (Lagurina) of Arvicolini (Pavlinov & Rossolimo 1987), Prometheomyini (Pavlinov et al. 1995), or Clethrionomyini (Mezhzherin et al. 1995). Following molecular phylogenetics (Fabre et al. 2012, Steppan & Schenk 2017) we classify lagurines as a subtribe; the divergence time estimate is 3.1 Mya (Abramson et al. 2021). In accordance with recent authors we distinguish 2 genera.

As far back as Merriam (1895), the Nearctic sagebrush vole *Lemmiscus curtatus* has long been classified as *Lagurus*. Kretzoi (1969a) suggested *Hyperacrius* is part of Lagurini.

Distribution. Open arid habitats (steppes, alpine pastures, semi-deserts and deserts) between Eastern Europe (Ukraine) and Central Asia (Mongolia and Chinese provinces of Xingjian, Gansu, Qinghai, and Inner Mongolia). Borders of distributional ranges are dynamic and a notable shrink was recorded over the last centuries.

Characteristics. The general appearance is lemming-like. Fur is long and soft, tail is short and densely clothed; feet are short and broad. Palms and plantae are thickly hairy, tubercles are much reduced or absent. Claws are strong but not elongated, shorter on hands; the thumb has a small nail (Figure 138). Eyes are large; ears are without antitragus, small and hidden in the fur. There are 8 nipples. Skull is short and broad with a convex dorsal profile. Zygomatic arches are powerful and moderately expanded and the rostrum is short and narrow. The interorbital region is moderately constricted with prominent, parallel supratemporal ridges separated by a deep medial sulcus. Squamosals have a prominent, peg-like postorbital process and the mastoid process of the squamosum bends outward; when viewed from the dorsal perspective the supramental triangle is wide and short; prelambdoid fenestrae (inferior and superior) are filled with bone. Bullae are large and partly filled with sponge bone; posteriorly they project to the level of occipital condyles or beyond. The external meatus is short and tubular and the mastoid chamber is inflated. From the lateral view the masseteric plate is comparatively long and the diastema exceeds the length of the upper molars (Figure 139). The posterior margin of the hard palate is of an arvicolini type (Pozdnyakov 2008); postero-lateral fossae are expanded and the medial crest is low. Pterygoid processes are short and the interpterygoid vacuity is comparatively wide (Figure 10g). The mandible shows no peculiarities. Of the incisors, the upper are strongly curved while the lower displace M_3 lingually, i.e. as is characteristic for Arvicolini. Molars are hypselondt, and without cement in re-entrant folds. Their appearance is long-drawn-out, with wide re-entrant folds and perfectly alternating salient angles. There are additional small salient angles ("vestiges of the protoconule" or "intermediate tubercles" sensu Hinton 1926a; "laguroid protuberance" in the terminology of Chaline et al. 1999) on the lingual re-entrant angle LR2 of the upper molars (frequently absent on M^3); these angles are unique for lagurines. Enamel differentiation is as in *Microtus* (s.lat.): thick leading edges are built of lamellar enamel while thin trailing edges are of radial enamel (Koenigswald 1980). Grinding pattern in upper molars (M^3 in particular) superficially resembles that of *Alticola*. M_1 has 4–5 closed triangles between the anterior lobe and the posterior cap; triangles of M_2–M_3 are only slightly reduced (Figure 140).

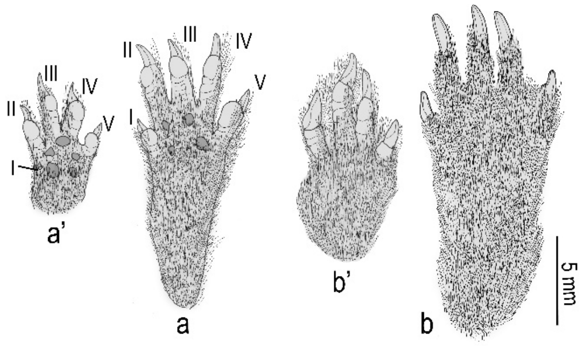


Figure 138: Left palm (a',b') and sole (a,b) in *Lagurus lagurus* (a,a') and *Eolagurus luteus* (b,b').

Key to genera and species

1a) Small (BWt ≤40 g; CbL≤25 mm; M_1 length≤2.75 mm); dorsal medial stripe present; angular process of mandible of normal length and not markedly turned outwards; PC on M^3 with 2 salient angles behind T4 (LS4 and BS4); M_1 with comparatively deep re-entrant angles anterior to T5 (BR4 and LR5) …..……………………………….... *Lagurus lagurus*
1b) Large (BWt >40 g; CbL>28 mm; M_1 length≥2.60 mm); adults without dorsal medial stripe; angular process of mandible short and turned outward; heel on M^3 simple without salient angles behind T4; M_1 without lingual re-entrant angle (LR5), the alternating BR4 is absent or shallow ……….…..................... 2 (*Eolagurus*)
2a) Ventral fur shaded buff; thumb with a small and pointed claw; bulla is approximately the same length as MxT; tubular meatus short; *porus acusticus* small and positioned away from squamosal root of zygomatic arch ………………………………………………… *E. luteus*
2b) Ventral fur white; thumb with a large and blunt claw; bulla longer than MxT; meatus tubular and turned forwards; *porus acusticus* large and positioned close to squamosal root of zygomatic arch ….....… *E. przewalskii*

GENUS: *Lagurus* Gloger, 1841 – Steppe Lemmings

Lagūrus Gloger, 1841:97. Type species by subsequent designation (Thomas 1895:192): "*Myodes lagurus*, Pall[as]" (=*Lagurus lagurus*).

Synonyms. *Eremiomys* Polyakov, 1881.

Taxonomy. A monotypic genus. Earlier also included *Eolagurus* (see below) and the Nearctic *Lemmiscus* (see under Lagurina).

Lagurus lagurus (Pallas, 1773) – Steppe Lemming

Distribution (Figure 141). Range extends to 2,801,448 km² of steppe snd semi-desert landscape between the Lower Dnepr River (Ukraine) in the west and southern Siberia (Republic of Tyva, Russian Federation), western Mongolia and north-western Xinjiang (China) in the east, also encompassing southern Russia and northern and central Kazakhstan. Northern border mainly follows the 55th parallel (confluence of the Volga–Kama Rivers in the west until the Novosibirsk Region and Khakassia in the east) with very few records reported further north (up to the 56th parallel in Tyumen Oblast). The line connecting Sea of Azov–Caspian Sea–Aral–Lake Balkhash marks the southern border. Between Balkhash and Zaysan the range turns southward reaching the Tien Shan Mts. (to the south of Issyk-Kul Lake, Kyrgyzstan) and Xinjiang. For details see accounts on subspecies.

The Quaternary range was more extensive reaching France and England in the west (Kowalski 2001) and northern Ural, Kemerovo region, middle Yenisey, north-western Altai and the Baikal in Asia (Dupal 2014). During the final stage of the Atlantic period (c. 5.2 kya), steppe lemmings were still among the most abundant small mammals on the Asiatic side of the Southern Urals (Kuzmina & Ulitko 2021). Populations fluctuate widely and steppe lemmings expand the range at high densities (Sludskiy et al. 1978). While in the mid-20th century the steppe lemming was still designated as "one of the most

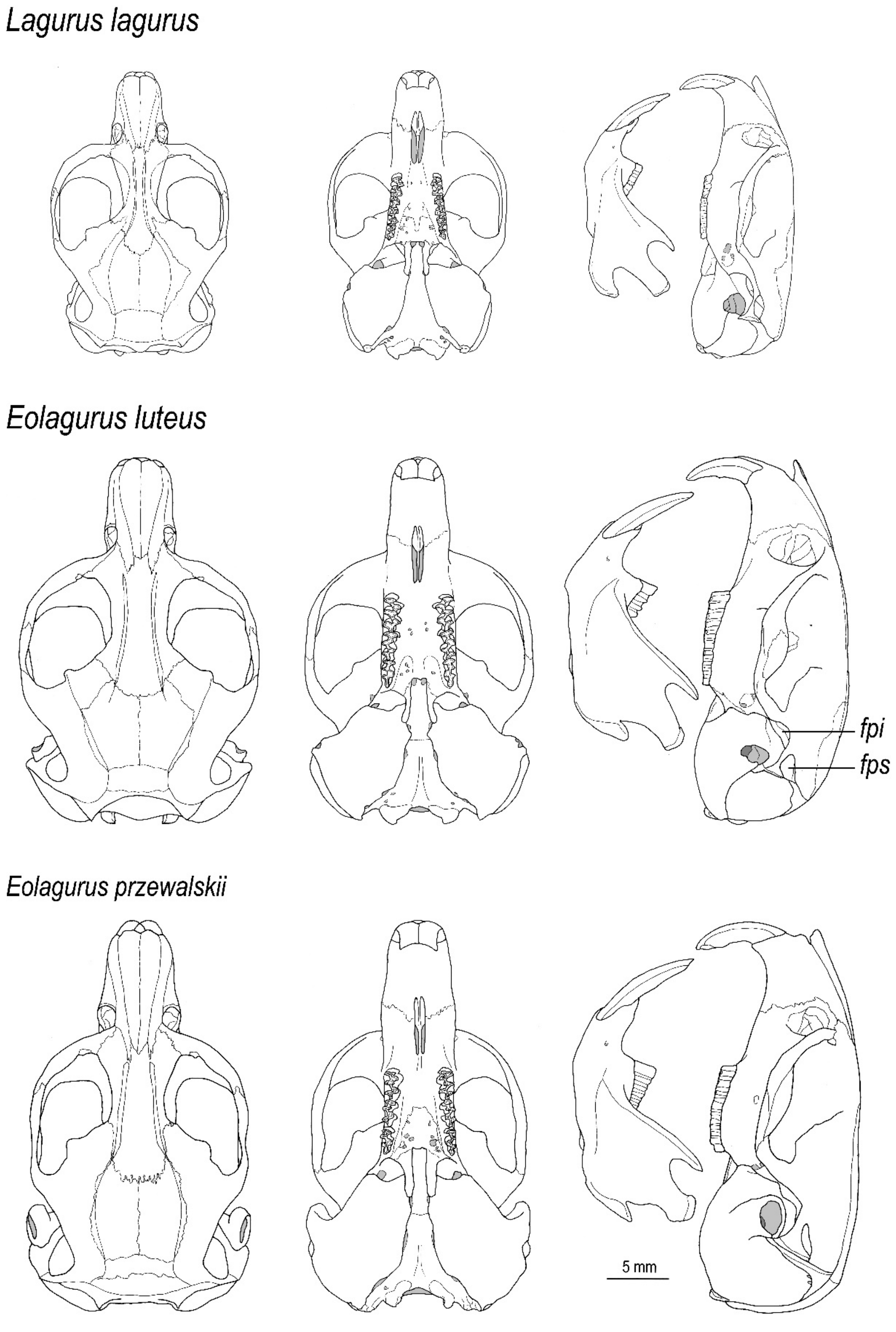


Figure 139: Skull and mandible in lagurines (top-to-bottom): *Lagurus lagurus* (from Cherijkovo, Luhansk, Ukraine), *Eolagurus luteus* (Markakolsky Rayon, Kazakhstan), and *E. przewalskii* (Tost-Ula, Mongolia). Praelambdoid fenestrae: *fpi–fenestra praelambdoidea inferior*; *fps–fenestra praelambdoidea superior.*

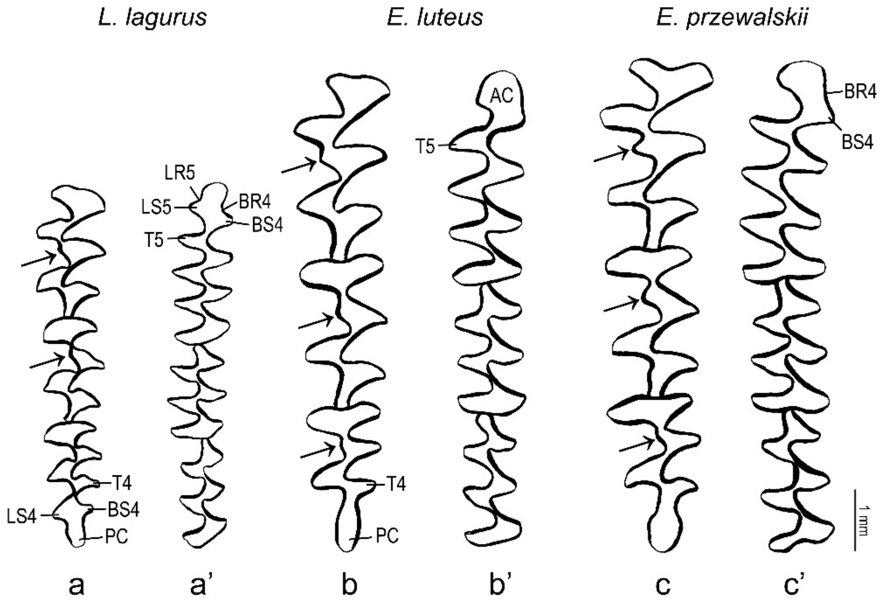


Figure 140: Molar pattern on upper (a–c) and lower molar rows (a'–c') in lagurines: *Lagurus lagurus* from Lake Uchum, Krasnoyarsk krai, Russian Federation (a,a'); *Eolagurus luteus* from Zaysan District, Kazakhstan (b,b'); *E. przewalskii* from Qaidam, China (c,c'). Arrows indicate the "laguroid protuberance" on the lingual re-entrant angle LR2 of the upper molars.

widespread and most abundant … rodents in Kazakhstan" (Karaseva 1963:198) and was capable of reducing the primary productivity in pastures of Yinjiang (by 30–40%; Luo et al. 2000), no high densities have been reported since the mid-1950s in Khakassia (Yudin et al. 1979), and the range shrank in the west. To the west of Dnepr (the Kiev and Odessa Regions of Ukraine) the steppe lemming was still present in the 1920s but disappeared shortly afterwards; some territories on the left bank of the Dnepr River (Poltava, Dnepropetrovsk and Zaporozhye Regions) were likely lost by the mid-20th century (Zagorodniuk 2009), whereas in others (e.g. Kherson Region) the steppe lemming still persists. It vanished from the trans-Volga semi-deserts during the early 1970s (Bukhareva & Bykov 2019) and a population collapse was recorded north of the Caucasus at approximately the same time (Tertyushnikov & Likhovid 2013).

Characteristic habitat is xeric steppe with sparse grass; dense vegetation and shrubs are avoided. Altitudinal range is from –20 up to 3,370 m a.s.l (Tien Shan Mts.).

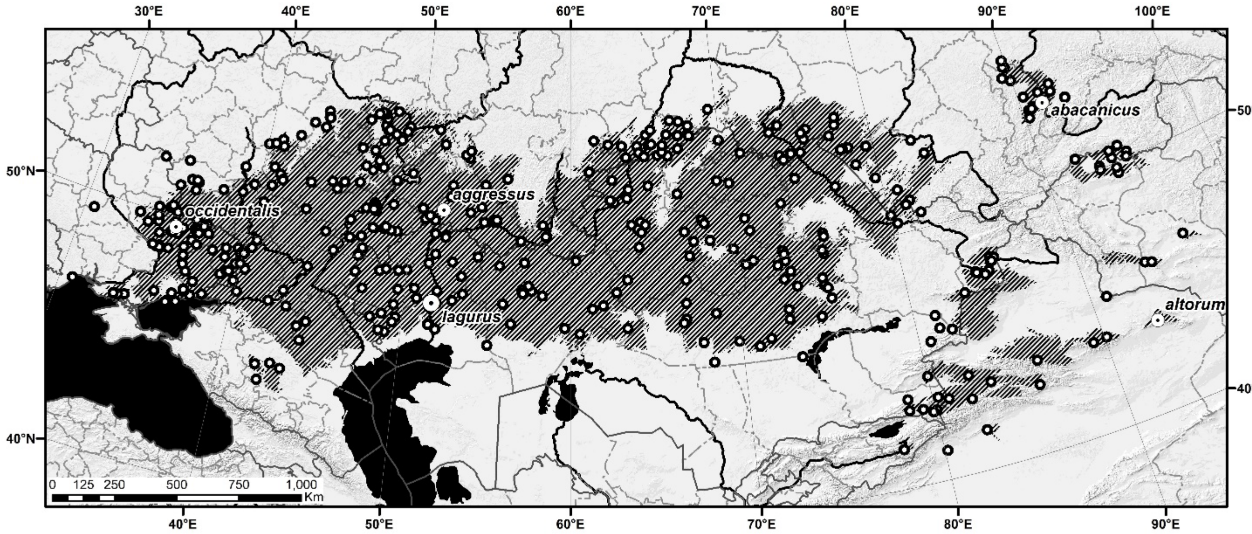


Figure 141: Distributional range of the steppe lemming *Lagurus lagurus*.

Characteristics (Figure 142). A small and slender lagurine with a distinct black stripe extending from the frontal or parietal region to the tail base; rarely does the stripe fade on the posterior back. Tail is short (TL/H&B=0.09–0.14) and densely covered with hairs which conceal the annulation; there is a long terminal pencil. Ears are small and hidden in the fur, but still decidedly larger than in *Eolagurus*. Toes are broad with short but powerful claws; the front thumb has a flat nail. Soles are thickly hairy. There are 5 relatively large palmar pads while only the anterior 4 small subdigital plantar pads are present (Figure 138a). In females, the pectoral and inguinal pairs of nipples are packed closer together than in other voles (Popov 1977). The baculum is larger relative to overall size than in *Eolagurus*. The shaft is on average 2.88 mm long and 1.11 mm wide. The trident ossifies and the medial digit is 0.76 mm long (Dearden 1958). The skull is widest at the zygomatic arches (ZgW/CbL=0.58–0.65); it is moderately deep with a flat dorsal profile behind the nasals. Viewed from above, the anterior edges of the zygomatic arches form an almost right angle at the junction with the rostrum. Nasals are short and supratemporal ridges are prominent. Incisive foramina are wide and frequently elliptical; they are situated in the middle of the diastema. Bullae are comparatively small and do not project behind the level of the occipital condyles. The mandibular body is rather shallow; the angular process is of normal length and not markedly turned outward. Molars are more complex than in *Eolagurus*; M^3 has a heel with 2 salient angles (LS4 and BS4) behind T4. On M_1 the salient angles anterior to T5 (BS4 and LS5) are prominent although widely confluent with PC; rarely are the anterior re-entrant angles BR4 and LR5 deep enough to nearly isolate the anterior cap. M^3 and M_1 morphotypes are detailed in Maleeva & Nordstrem (1976) and Pozdnyakov & Senotrusova (2006). Karyotype: 2n=54, NF_a=58–60; the difference in the fundamental number is due to the largest autosomal pair which is either acrocentric or subtelocentric; X is large metacentric and Y is small acrocentric (Zima & Král 1984).

Variation and subspecies. The diversity of M^1 morphotypes was higher during the Late Pleistocene than now (Maleeva 1976). There is an obvious longitudinal trend in size (larger in the east) and colouration (darker to the west, lighter to the east). Genetic distances among samples from European Russia, western Siberia, Kazakhstan, and Mongolia are nevertheless low (Bannikova et al. 2019). Differences in the centromeric position of the largest autosome (and consequently in NF_a) were associated with a subspecific division: NF_a=60 in *lagurus* and *aggressus*; NF_a=58 in *altorum* and *abacanicus* (Zima & Král 1984). Following Serebrennikov (1929) and Ognev (1950) we recognise 4 subspecies. Although reasonably well-differentiated in colouration, transitional zones between them have not yet been studied.

Figure 142: Steppe lemming *Lagurus lagurus*. Photo: Christian Montermann

Lagurus lagurus lagurus (Pallas, 1773)

Mus lagurus Pallas, 1773:704. Type locality: “ad Iaȉkum rarius australiorem, copiosissima vero in campis arenosis herbidis ad Irtin, inque deserto tatarico” (p.705), restricted to “steppes around Yaik [=Ural River]”, Kazakhstan (Serebrennikov 1929:264).

Distribution. Northern Caucasus (Stavropol'), plains of Kazakhstan (West Kazakhstan, Atyrau, Aqtöbe, Qostanay, North Kazakhstan, Aqmola, Pavlodar, Karaganda and northern part of East Kazakhstan Regions), and southern part of Western Siberia between Volga and Ob’ Rivers (Kalmykia, Astrakhan', Chelyabinsk, Kurgan, Tyumen', Omsk, Novosibirsk Regions and Altai Krai; all in Russia).

Characteristics (Figure 143). Overall appearance is light; dorsal pelage is light-brown, hazel-brown, drab or cinnamon-buff, shaded grey; mid-dorsal stripe is dark-brown or grey-brown, narrow, ill-defined in some individuals. Underside is greyish-white, shaded buff; transition on the flanks is blurred. The tail is uniformly whitish, shaded buff; feet are white or buffy-white. Winter pelage is longer and silkier and the shade is more buff. Young are greyer and less bright. Dimensions: BWt=18–40 g, H&B=97–125 mm, TL=7–15 mm, HF=11.5–15 mm, EL=5–7 mm, CbL=21.8–23.8 mm, ZgW=13.2–15.0 mm, MxT=5.4–6.2 mm.

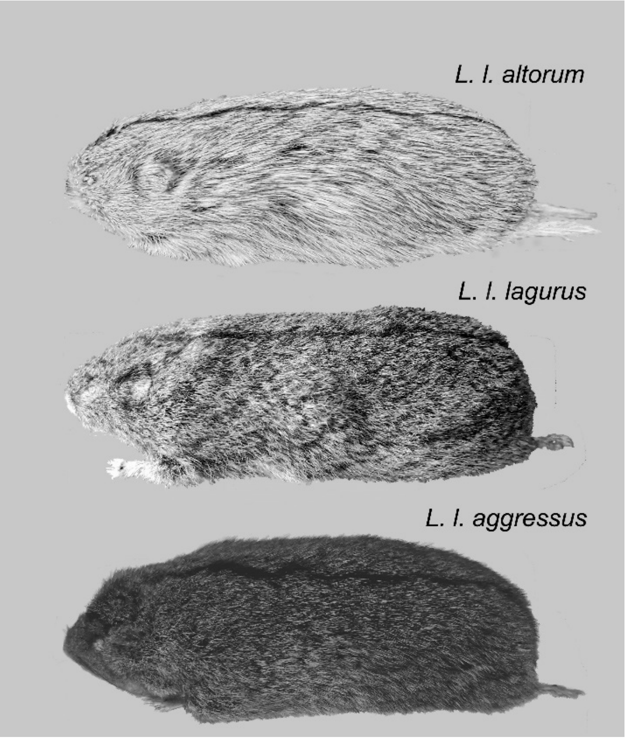


Figure 143: Subspecies of *Lagurus lagurus*, arranged from the palest (top) to the darkest (bottom): *L. l. altorum* (Tuva Region, Russia), *L. l. lagurus* (Semey, Kazakhstan), and *L. l. aggressus* (Buzuluk District, Russia). Photo: B. Kryštufek.

Lagurus lagurus altorum Thomas, 1912

Lagurus lagurus altorum Thomas, 1912b:401. Type locality: “Barlik [Barkol] Mts., N.W. Dzungaria. 6000’ [1,280 m]”, Xinjiang, China.

Distribution. Several small isolates in the east: (i) Uvs-Nur Depression in souther Tuva (Russia) and Uvs Aymag (Mongolia); (ii) southern Mongolian Altai (Govi Altay), Baytag-Bogdo (Hovd, south-western Mongolia) and north-eastern Xinjiang (China); (iii) Tarbagatay and Dzhungarian Alatau on the border between Kazakhstan (Almaty and south-eastern East Kazakhstan Regions) and China (noth-western Xinjiang), and (iv) the Tien Shan Mts. in Kazakhstan (Almaty Region), Kyrgyzstan (Ysyk-Köl Region) and China (Xinjiang).

Characteristics (Figure 143). A large subspecies with light pelage. Dorsal fur is smoke-grey to drab-grey, paler on flanks; ventral side is greyish-white, shaded buff in some individuals. Mid-dorsal stripe usually narrow, sometimes blurred in its posterior half. Dimensions: BWt=21–40 g, H&B=84–125 mm, TL=7–16 mm, HF=10–17 mm, EL=3–7 mm, CbL=21.4–26.7 mm, ZgW=12.8–16.2 mm, MxT=5.3–7.3 mm.

Lagurus lagurus aggressus Serebrennikov, 1929

Lagurus lagurus aggressus Serebrennikov, 1929:267. Type locality: “Ferapontovka, distr[ict] Busuluk [Buzuluk], gouv. [Guberniya] Samara”, now in Orenburg Oblast, Russian Federation.

Synonyms. *Lagurus lagurus occidentalis* Migulin, 1938; *[Lagurus lagurus]* morpha *complexus* Bazhanov, 1930 [unavailable]; *L[agurus] lagurus aggressus* natio *saturatus* Ognev, 1950 [unavailable].

Taxonomy. The *occidentalis* was recognised as a subspecies in its own right (Zagorodniuk 2009:79), or was synonymised with either *aggressus* (Ognev 1950:575) or the nominal subspecies (Bulakhov & Pakhomov 2006:161).

Distribution. Ukraine (Sumy, Kharkiv, Kherson, Donetsk and Luhansk Regions) and parts of European Russia (Ryazan', Lipetsk, Kursk, Voronezh, Rostov, Tambov, Nizhniy Novgorod, Mordovia, Penza, Chuvashia, Ulyanovsk, Tatarstan, Samara, and Bashkortostan Regions). For presence in Kazakhstan (to the east of the Ural Mts.) see Kuznetsov (1948b).

Characteristics (Figure 143). The darkest subspecies. Dorsal, cheeks and flanks are dark-brown or hair-brown, shaded dark-grey, rarely clove-brown, buffy-brown or olive-brown; individual variation in colour is substantial. Mid-dorsal stripe is usually wide, narrowed in some animals or distorted by blackish hair on the midback which is most evident in very dark individuals. Ventral side is pale brownish yellow to greyish with wood-brown tints. Tail is uniformly olive-buff to bi-coloured (dark above, yellowish-grey below). Winter pelage is longer and thicker with a more intense rusty shade. Young are greyish-brown. Dimensions: BWt=19–40 g, H&B=73–115 mm, TL=6–16 mm, HF=11–16 mm, EL=4–7.5 mm, CbL=20.2–25.0 mm, ZgW=12.6–15.3 mm, MxT=5.3–6.6 mm.

Lagurus lagurus abacanicus Serebrennikov, 1929

Lagurus lagurus abacanicus Serebrennikov, 1929:267. Type locality: "Dmitrievka, distr[ict] Minusinsk, Siberia", Khakassia, Russian Federation.

Distribution. Minusinsk Depression in south-Central Siberia (Russia: Khakassia and southern Krasnoyarsk Krai).

Characteristics. A large subspecies: H&B=85–120 mm, TL=11–14 mm, HF=13–15 mm, EL=6.9–8 mm, CbL=24.7–26.8 mm, ZgW=15.3–17.3 mm, MxT=6.5–6.9 mm. Colour is intermediate between the nominal subspecies and *aggressus*. Dorsal side light-drab, flanks hazel-brown, ventral side light beige, paws light-grey; tail is bi-coloured, darker above, yellowish-white below. Dental fields compressed (most notably on upper molars).

Genus: *Eolagurus* Argyropulo, 1946 – Desert Lemmings

Eolagurus Argyropulo, 1946:44. Proposed as a subgenus for "*Eolagurus luteus* and *Eolagurus przevalskii* (sic)". Type species by subsequent designation is "*Lagurus luteus* Eversmann" (Corbet 1978:166).

Characteristics. Moderately large and chunky voles with large eyes, very short ears (which lack antitragus), long whiskers, and a short tail. Feet robust, soles densely hairy with the fringes of stiff hair on the outer side of the feet; hairs conceal pads. Pelage is yellowish, shaded brown, rusty or grey. Skull is deep, widest at the mastoids and auditory meatus. In the dorsal plane the anterior edges of zygomatic arches form an oblique angle at the junction with the rostrum. Incisive foramina are narrow and their anterior margin is shifted backward. Bullae are much inflated and the mastoid portion expands beyond the plane of condyles. The mandibular body is deep; the angular process is blunt and turned outward. M^3 has a simple heel behind T4. The anterior cap of M_1 is of simple shape, either circular or oval; 4th buccal re-entrant angle BR4 absent or shallow, the LR5 is absent.

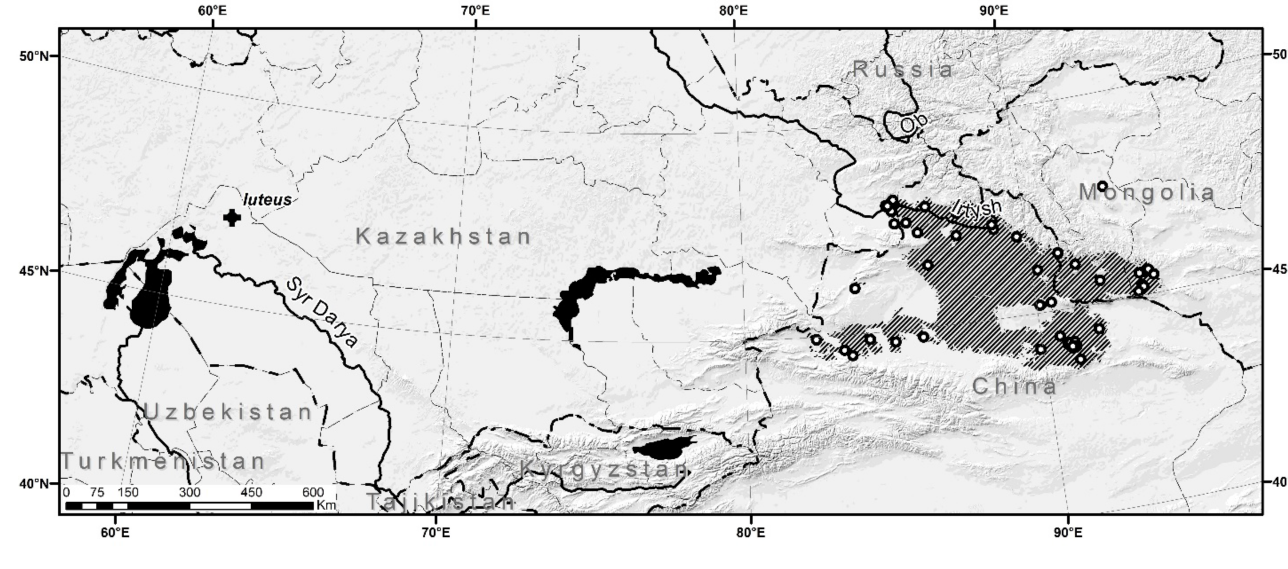


Figure 144: Distributional range of the yellow desert lemming *Eolagurus luteus*.

Eolagurus luteus (Eversmann, 1840) – Yellow Desert Lemming

Georychus luteus Eversmann, 1840:25 + plate II. Type locality: "northwestern shore of the Aral Sea"; restricted to "Kzyl-Ordinskaya obl[ast]" (Pavlinov & Rossolimo 1987: 187), Kazakhstan.

Taxonomy. Frequently reported under the generic name *Lagurus* (see comments on Lagurina). Based on molecular clock estimates, *luteus* and *przewalskii* split at the Early/Middle Pleistocene boundary at 1.060 Mya (CI=0.658–1.708 Mya; Bannikova et al. 2019).

Distribution. (Figure 144). A range of 184,172 km^2 covers the Zaisan Depression in eastern Kazakhstan, the Dzungarian Govi Desert in Mongolia, and the Junggar Basin (Dzungaria) in northern Xinjiang (China) as far south as the Tien Shan Mts; an isolated occurrence in the southern part of the Great Lakes Depression (north-western Mongolia) was reported only recently (Bannikova et al. 2019). Altitudinal range is 250–2,170 m a.s.l.

The historical range was more extensive. During the Late Pleistocene, *E. luteus* occurred at the Black Sea coast of Romania (Petculescu & Ştiucă 2008), in Moldova and Ukraine reaching the Kama River and the upper Ob', the Kuznetsk Basin (south-western Siberia), north-western Altai, eastern Sayan, the Pamir Mts. in the south, and the Trans-Baikal region in the east. East of the Urals, the northern border was at the 55–57th parallel (Maleeva 1973, Dupal 2005). During the Early Holocene the yellow lemming was still present in Crimea and persisted to the west of Astrakhan until the 8–10th century A.D. (Maleeva 1970). In the past it was abundant in sandy habitats to the south of the line connecting the northern Caspian Sea–Sea of Aral–Balkhash Lake (i.e. ~47th northern parallel), locally even spreading northwards (e.g. 170–230 km north of Balkhash) and reaching Kazakh Upland in the south (Sludskiy et al. 1978). Eduard A. Eversmann (1784–1860) and his contemporaries still collected *E. luteus* along the Ural River, in Ustyurt, Karakum nearby Aral, and on Lake Balkhash (Kuznetsov 1948b), i.e. up to ~2,300 km westward of its current range. As in other lagurines, populations oscillate greatly which can lead to regional extinctions during marked depressions (Ismagilov & Bekenov 1969). Other clues, e.g. epizootics or a series of several severe winters (1879–1892) were also blamed for the sudden disappearance of *E. luteus* from the majority of Kazakhstan in the mid to late 19th century (Sludskiy et al. 1978). On the other hand, range expansions were rapid at peak densities; e.g. Afanasiev et al. (1953:253) reported that in the 1940s there had been a long-distance migration "across tens and even hundreds of kilometres" in a matter of several months. The yellow desert lemming inhabits arid areas on clay, sands and saline soils with sparse shrubs (*Artemisia*, *Eurotia*) and grasses. Preferred habitats are river valleys, lake depressions and similar humid places up to 2,100 m a. s. l.

Description (Figure 145). Dimensions: BWt=42–130 g, H&B=105–175 mm, TL=15–24 mm, HF=16–22 mm, EL=4–7 mm, CbL=28.4–36.2 mm, ZgW=17.3–22.1 mm, MxT=6.7–9.0 mm. Tail is relatively longer (TL/H&B=0.09–0.20) than in *przewalskii;* densely clothed with hair which conceals the annulation; hairs terminate in a prominent pencil (length=5.5–8.5 mm). Thumb has a small and pointed claw. Fur is soft, 11–12.5 mm long, slate at base. Dorsal fur is rusty-brown or yellow-brown, black at the tips and shaded grey in some individuals; flanks are ochraceous, drab or yellowish, belly is cream or yellowish and clouded with slate underfur; there is no clear demarcation along the flanks. Cheeks are yellowish; paws, tail and muzzle are yellowish-white. Juveniles have a mid-dorsal black stripe when 3–11 days old (Sludskiy et al. 1978) which disappears by weaning. Baculum: the shaft (length=2.89 mm) is wider across the base (width=1.29 mm) than in *Lagurus*; the distal tip of the shaft is broadly deltoid. Only the basal part of the central distal digit is ossified; it has approximately the same width as length (Dearden 1958). Skull is deeper and wider (ZyW/CbL=0.58–0.69) than in *przewalskii;* dorsal profile bends evenly. Auditory bullae are smaller (length of bulla<MxT) compared to *przewalskii* and the meatus is shorter; *porus acusticus* is small and shifted away from the squamosal root of the zygomatic arch (Figure 139). Posterior cap on M^3 tends to be longer and the anterior cap on M_1 is more circular than in *przewalskii* (Figure 140). Karyotype: 2n=56, NF_a=54; with the exception of one subtelocentric pair

Figure 145: Yellow desert lemming (*Eolagurus luteus*) from Mulei (Mori), Xinjiang, China. Note the upright position in right-hand inset which is atypical for arvicolines. Photo: G. Shenbrot.

all the autosomes are acrocentric; X is submetacentric and Y is acrocentric (Orlov et al. 1978).

Variation and subspecies. Monotypic. Size varies between years; males are heavier by 15% at high population densities (Sludskiy et al. 1978).

Eolagurus przewalskii (Büchner, 1889) – Przewalski's Desert Lemming

Eremiomys przewalskii Büchner, 1889:127. Syntypes are from "Gass, Zaidam" and "Zaidam"; type locality subsequently restricted to "Lake Ikhe-Tsaydamin-nur

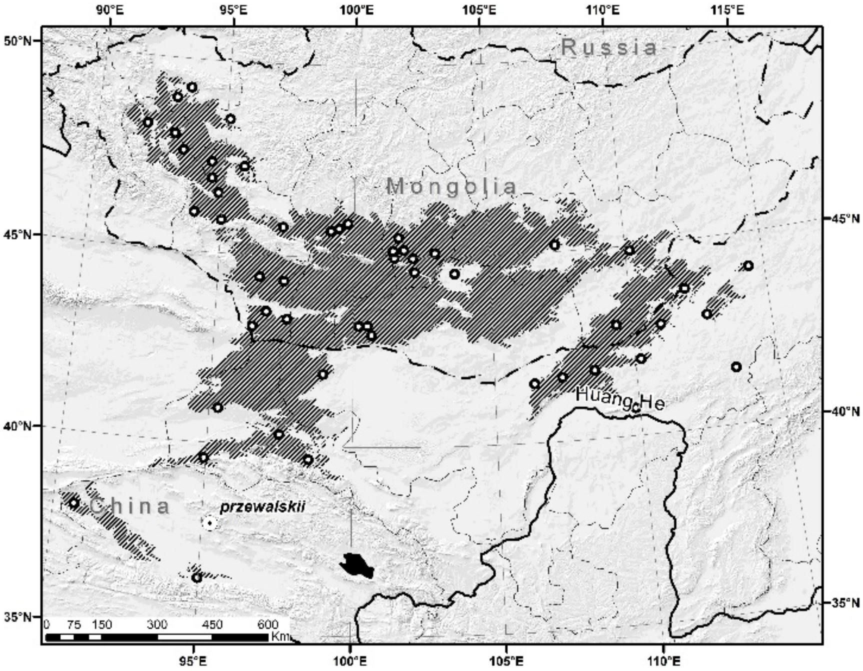


Figure 146: Distributional range of Przewalski's desert lemming *Eolagurus przewalskii*.

[Iche-Qaidamin Nor], Tsaydam [Qaidam], northern Tibet", China (Bannikov 1954:492).

Taxonomy. In the past *przewalskii* was frequently synonymised with *luteus*. Its species status is evident from morphological, karyological and molecular evidence (reviewed in Bannikova et al. 2019).

Distribution (Figure 146). Deserts and semi-deserts in the Great Lakes Depression, Valley of the Govian Lakes, Northern Govi, Eastern Govi, Trans Altai Govi Desert, and Alashan' Govi Desert in Mongolia and northern China: south-central Inner Mongol (from Ejin Qi to Shangdu), north-western Gansu, and north-western Qinghai. Despite an extensive distributional range (584,296 km^2), findings of this species are scarce. Characteristic habitat is on clay, sandy or gravel soils sparsely covered with shrub and grass; depressions of river banks and beds are preferred. As in other lagurines, population numbers oscillate widely. E.g. in 1947, Przewalski's desert lemmings were excessively abundant in Khuysin-Govi (Mongolia) where Bannikov (1954) had not been able to find a single individual 3 years earlier. Altitudinal range is 910–3,150 m.

Characteristics. Dimensions: BWt=57–85 g, H&B=112–142 mm, TL=11–18 mm, HF=18–23 mm, EL=4–6 mm, CbL=30.5–35.7 mm, ZgW=17.3–21.7 mm, MxT=7.1–9.5 mm. Tail is relatively shorter (TL/H&B=0.08–0.14) than in *luteus,* densely hairy and with a prominent pencil (length=5.5–11 mm). Thumb claw is large and blunt. Fur is soft, 8.5–17 mm long; back is sand-yellow, drab-grey or light brown, belly, paws, tail and muzzle are white, demarcation along flanks is quite distinct. Hair bases are slate dorsally, grey or exceptionally white bellow; dorsal fur has blackish-brown tips. Skull shallower and narrower (ZyW/CbL=0.56–0.61) than in *luteus;* auditory bullae larger (length of bulla>MxT). Meatus is tubular, long, and turned forward; *porus acusticus* is large and close to the squamosal root of the zygomatic arch (Figure 139). Heel on M^3 tends to be shorter and the anterior loop on M_1 is more oval (Figure 140). Karyotype: 2n=60, NF_a=58; all autosomes are acrocentric; X is submetacentric and Y is the smallest acrocentric (Bannikova et al. 2019).

Variation and subspecies. Monotypic species.

SUBTRIBE:
Hyperacrina New Subtribe

Taxonomy. In the past *Hyperacrius* was classified in tribe Clethrionomyini (Hooper & Hart 1962, Gromov & Polyakov 1977, McKenna & Bell 1997) or Lagurini (Kretzoi 1969a). Pozdnyakov (2008) and Kohli et al. (2014) left tribal affiliation open while Robovský et al. (2008) regarded *Hyperacrius* as one of the basal arvicolines along with *Ellobius, Prometheomys* and Lagurina. In a multi-locus phylogenetic analysis, Tang et al. (2018) questioned whether *Hyperacrius* indeed belongs to Clethrionomyini and subsequent studies classified it as a sister group to Microtina (e.g. Abramson et al. 2021). Since the genus is genetically and morphologically well set-apart from all other Arvicolini, it is allocated to a new subtribe.

Type genus. *Hyperacrius* Miller, 1896.

Diagnosis and Comparisons. Hyperacrina new subtribe belongs to Arvicolini as evident from the structure of the posterior palate (Figure 10f) and a 16,341-*bp* long alignment of *Mt*-DNA (Abramson et al. 2021). On the other hand, Hyperacrina differs from all known subtribes of Arvicolini in *Mt*-sequences and in a combination of external and craniodental traits. Although members of the new subtribe are highly fossorial, they clearly contrast Bramina. In Hyperacrina (i) the ears are normally developed (reduced in Bramina); (ii) there are 5 plantar pads and 2 pairs of inguinal nipples (6 pads and 1 pair of inguinal nipples in Bramina); (iii) the front feet are distinctly smaller and the thumb is negligible (in Bramina, front paws are nearly the same size as the hind feet, and the thumb is decidedly larger); (iv) the skull has the shape and proportions of Microtina (e.g. incisive foramens are long; skull is aberrant in Bramina with very short incisive foramens); (v) the alveolar process is rather feeble (heavy in Bramina). Hyperacrina has molars with a simple grinding pattern and confluent dental fields while triangles normally alternate in Pliomyina, Lagurina, Arvicolina and Microtina.

Content. The new subtribe contains the genus *Hyperacrius* Miller, 1896, with 2 recent species (see below).

GENUS: *Hyperacrius* Miller, 1896 – Kashmir Voles

Hyperacrius Miller, 1896: 54. Type species: *Arvicola fertilis* True.

Taxonomy. Miller (1896) proposed *Hyperacrius* as one of 12 subgenera of *Microtus* which also included all current Clethrionomyina except *Clethrionomys*. At that time Kashmir voles were regarded as "a peculiar descendant from some form of *Alticola*" (Hinton 1926a:44) "modified for a more strictly underground life" (Miller 1896:55) and were occasionally reported under the (sub)generic name *Alticola* (Sclater 1891). Wroughton (1920) still split Kashmir voles between *Hyperacrius* and *Alticola* (both as a subgenera of *Microtus*) until Hinton (1926a) elevated *Hyperacrius* to a genus in its own right and defined its taxonomic scope.

Distribution. Kashmir voles occupy higher altitudes (usually >1,800 m) along the southern slopes of the Himalayas, on both sides of the Indus River between the Pakistan–Afghanistan border and the Vale of Kashmir in India. Ranges are fragmented. The 2 species are parapatric except for Shogran (Kagan Valley, Pakistan) where *H. fertilis* was found "often within a meter's distance from *H. wynnei*" (Traub & Evans 1967:651). Recent range (~420 km east-to-west and ~250 km north-to-south; Phillips 1969) is one of the smallest in any subtribe of Arvicolini. An Early Pleistocene record in Huairou County, north of Beijing, China (Huang & Guan 1983), suggests a much wider Quaternary distribution of *Hyperacrius*. Taxonomic interpretation of the fossil material should be approached with some caution, however (Pozdnyakov 2008).

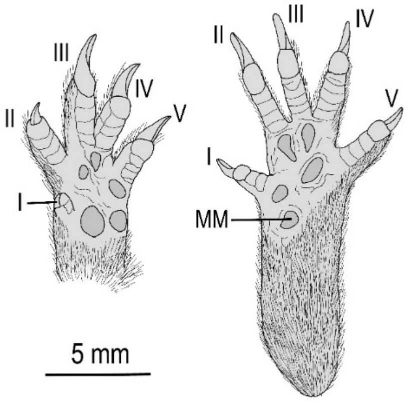


Figure 147: Left palm (a') and sole (a) in *Hyperacrius fertilis* (Jammu and Kashmir, India). Digits are indicated using Roman numerals (thumb=I). MM–medial metatarsal pad.

Characteristics. Small to moderately large fossorial voles modified for a subterranean life; tail is rather short (TL/H&B≈0.35–0.50). Head is bluntly rounded and eyes are small, presumably the consequence of hypertrophied temporal muscles (Hinton 1926a). Ears are normally developed, suborbicular, as wide as they are high, and usually hidden in the fur. Vibrissae are very short, hardly reaching the ears. Pads (5 plantar and palmar pads, respectively) are small; soles are hairy posterior to the metatarsal pad. Claws are well-developed but not particularly large; the thumb has a blunt claw (Figure 147). Tail is densely covered by hair which conceals the annulation and forms a modest terminal pencil. The secondary sexual dimorphism in size is not obvious (Phillips 1969). Fur is dense and soft, sometimes mole-like. Females have 1 pectoral and 2 inguinal pairs of nipples. Proximal baculum is slightly bent dorsally; a prominent proximal expansion bears

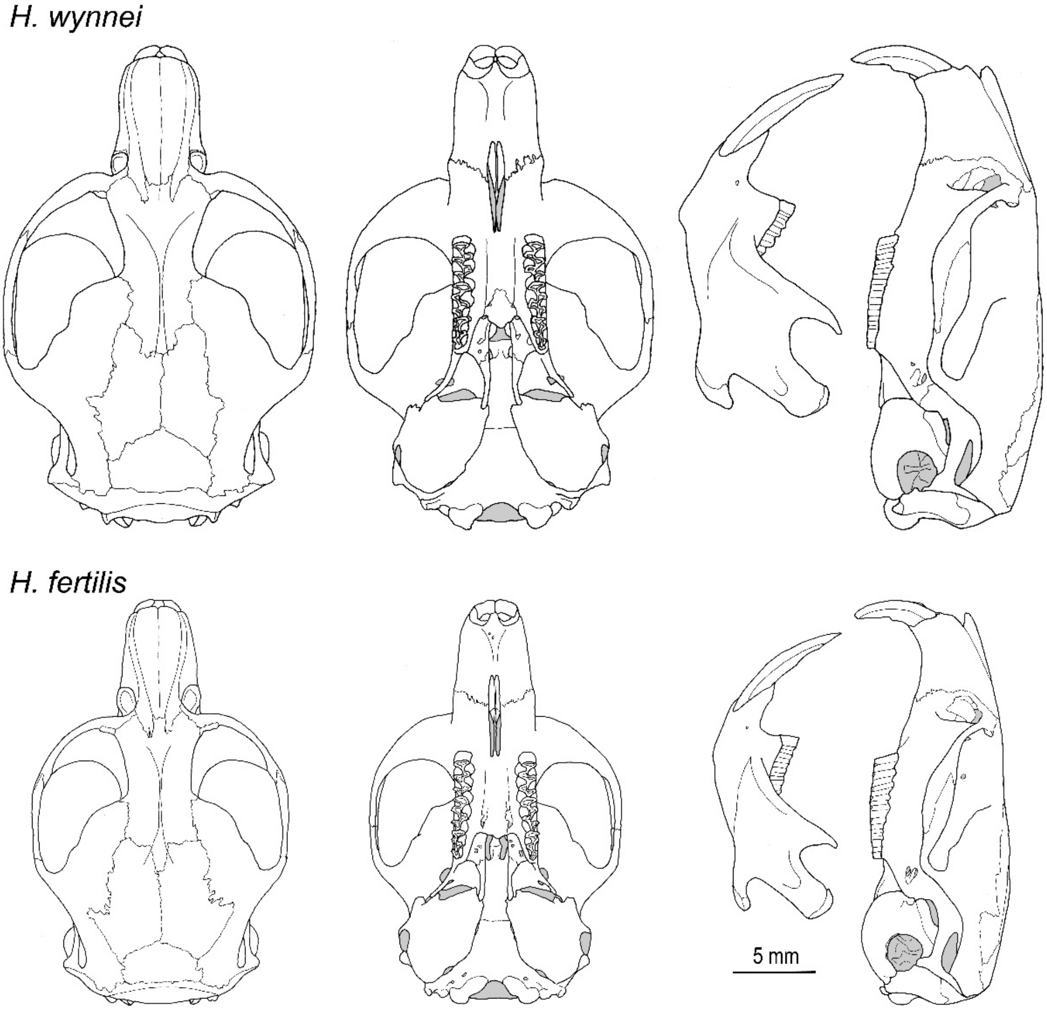


Figure 148: Skull and mandible in Kashmir voles: top–*Hyperacrius wynnei* (Pir Pinjal Range, Pakistan); bottom–*H. fertilis* (Khagan Valley, Pakistan).

basal tuberosities. Phillips (1969) who drew figures of this structure in both species did not mention the distal trident.

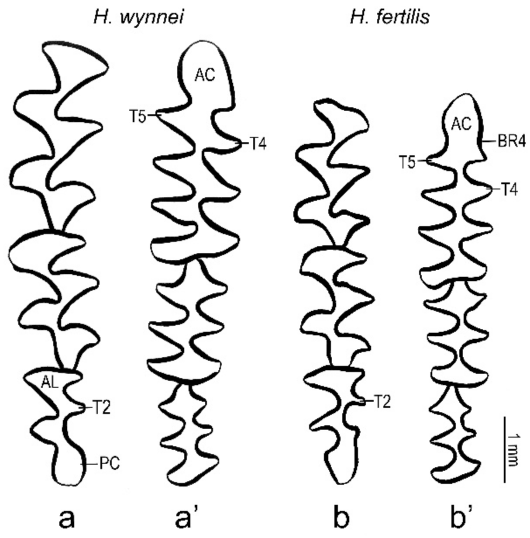


Figure 149: Molar pattern in Kashmir voles *Hyperacrius*. Pictured are upper (a,b) and lower rows (a',b') in *H. wynnei* (a–Pir Pinjal Range, Pakistan) and *H. fertilis* (b–Jammu and Kashmir, India).

Skull is shallow and short with abruptly spreading zygoma (ZgW/CbL$\approx$0.64–0.65). Rostrum is long, nasals wedge-shaped, braincase is relatively short, interorbital region is well-constricted, parietals are small and interparietal is proportionally large. Dorsal outline is evenly convex. Temporal ridges extend from the naso-maxillary suture back to the level of glenoid fossa; they fuse at an early age to form a median interorbital crest; lambdoid crest is prominent. The mandible is comparatively low; the root of the lower incisor tends to form a knob (alveolar process) below the articular process (Figure 148. The upper incisors are slightly proodont. Molars are lightly built, tall-crowned and rootless; re-entrant folds lack cement. Enamel is slightly thicker on the luff edge (0.06 mm) than on the lee edge (0.05 mm; in *fertilis*). Radial enamel prevails; lamellar type is present on the luff edges and primitive lamellar type on the lee edges; there is no tangential enamel (Koenigswald 1980). Posterior cap of M^3 resumes a semi-circular or oval shape; the antero-labial triangle T2 is reduced and assimilated into the anterior lobe. M_1: the anteroconid complex consists of confluent triangles T4–T5 and a simple anterior cap which may bear a shallow re-entrant angle BR4. M_2–M_3 have only 3 dental fields each (Figure 149). Karyotype is not known.

Key to species

1a) Fur short and stiff. Smaller: HF$\leq$19 mm, OnL$\leq$24 mm, MxT$\leq$6.4 mm; ears longer (usually 10–13 mm), tail proportionally shorter (TL/H&B<0.30). Baculum with narrow base, width-to-length ratio$\approx$1:2.5 …….…. *fertilis*
1b) Fur long and luxuriant. Larger: HF$\geq$19 mm, OnL$\geq$25.4 mm, MxT$\geq$6.2 mm; ears shorter (usually 8–10 mm), tail proportionally longer (TL/H&B>0.30). Baculum with wide base, width-to-length ratio$\approx$1:1.7 ………………………………………………………… *wynnei*

Hyperacrius wynnei (Blanford, 1881) – Murree Kashmir Vole

Distribution (Figure 150). Known from 3 small isolated areas in northern Pakistan (Swat and southern and central Kaghan valley); geographic range is extremely small (932 km^2). The majority of authors report *wynnei* also for Jammu and Kashmir (Agrawal 2000, Musser & Carleton 2005) and Himachal Pradesh (Alfred et al. 2002) in India. The only record for Jammu and Kashmir is Sardalla (altitude 2,650 m) and is based on a sample in the Natural History Museum London (Hinton 1926a); these animals are decidedly smaller (H&B=84–92 mm, HF=16–17 mm; Ellerman 1961) than *wynnei* and therefore fit the variation range of *fertilis*. Sardalla is frequently mentioned in compilations of Indian mammals though its exact position is undefined. Chakraborty (1983) placed the site in the District of Islamabad (Pakistan) while other authors provide no coordinates. We therefore consider the presence of *wynnei* in India to be unproven. Roberts (1997) also argued that *wynnei* is endemic to Pakistan.

The species occupies Himalayan moist coniferous (*Abies pindrow, Pinus wallichiana*) forests, clearings, scrubland, agricultural land and orchards at 1,830–3,290 m (Phillips 1969, Arshad 1991).

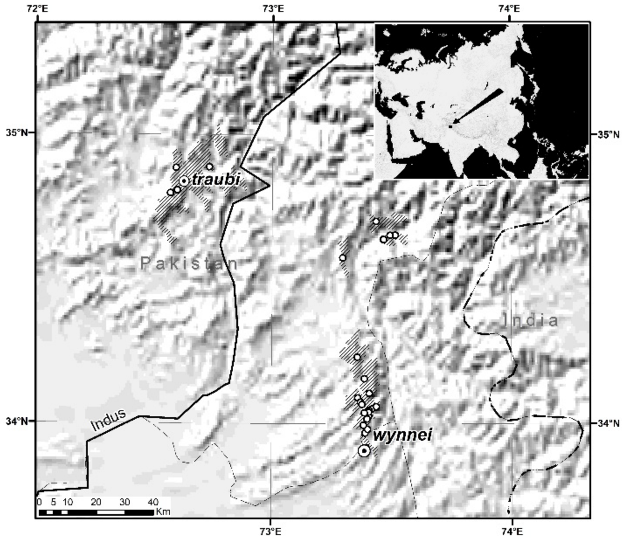


Figure 150: Distributional range of the Murree Kashmir vole *Hyperacrius wynnei*.

Characteristics. The larger species with long and relatively fluffy fur. Pelage is dark chestnut or dark rich brown with a slight greyish tinge; lower parts are light to slate grey, occasionally pale brown to cinnamon. Immature animals are a darker grey. Tail displays the same colour as the back and is indistinctly bi-coloured; feet are grey. Proximal baculum is short (length=2.5 mm) and wide (1.5 mm) with a bulb at the distal end and prominent basal tuberosities (Phillips 1969). Skull differs from the condition in *fertilis* in (i) a squarish braincase (length≈width; in *fertilis* length>width), (ii) wider nasals at the naso-frontal suture (narrower in *fertilis*), (iii) larger interparietal (length>½ width; in *fertilis* length≈½ width), (iv) smaller bullae (length of bulla<MxT; in *fertilis* length of bulla≈MxT), (v) deeper zygoma at the juncture of maxillary and squamosal processes (shallower in *fertilis*), (vi) more proodont incisors (in *fertilis* more orthodont), (vii) deeper and shorter mandible with longer and sickle-shaped coronoid process and robust angular process; in *fertilis*, mandible is shallower, coronoid process is shorter and blunt and angular process is slim (Figure 148). Molar pattern is as in the genus and apart from its larger size (MxT=6.2–7.2 mm) does not differ from *fertilis* (MxT=5.5–6.4 mm) (Figure 149).

Variation and subspecies. Light and dark coloured animals can co-occur (Roberts 1997). Phillips (1969) recognised 2 subspecies separated by a ~150 km wide gap created by the valley of Indus.

Hyperacrius wynnei wynnei (Blanford, 1881)

Arvicola wynnei Blanford, 1881a:244. Type locality: "Ad Mari (Murree) in montibus Himalayanis occidentalibus, ad latus occidentale fluminis Jhelum." Subsequently interpreted as "Murree, 7000 ft [2,135 m], North Punjab (border of Rawalpindi-Hauara districts) West Pakistan" (Phillips 1969:462).

Distribution. Upper Kaghan Valley, Hazara, Pakistan.

Characteristics. Larger: BWt=42.5g; HTL=141–151 mm (H&B=99–116vmm), TL=27–45 mm, HF=17–21 mm, EL=8–11 mm, OnL=26.1–27.9 mm, ZgW=16.8–17.9 mm, MxT=6.5–7.4 mm.

Hyperacrius wynnei traubi Phillips, 1969

Hyperacrius wynnei traubi Phillips, 1969:463. Type locality: "Yakh Tangai, 6600 ft [2,010m], Swat, West Pakistan".

Distribution. Swat, Khyber Pakhtunkhwa, Pakistan.

Characteristics. Smaller: HTL=133–149 mm, TL=30–34 mm, HF=19–20 mm, EL=8–10 mm, OnL=24.5–25.9 mm, ZgW=15.7–17.1 mm (Phillips 1969).

Hyperacrius fertilis (True, 1894) – True's Kashmir Vole

Distribution (Figure 151). Northern Khyber Pakhtunkhwa (Dir, Swat, areas of the Kaghan Valley and Nanga Parbat, Pir Panjal), Azad and Jammu Kashmir (Pakistan); also Khistwar (Jammu and Kashmir) in India. *H. fertilis* occurs at higher elevations (2,100–4,500 m) than *wynnei* and lives in alpine meadows, cultivated areas, pastures, and clearings adjacent to forests (Phillips 1969; Awan et al. 2004 [reported as *wynnei*]). Geographic range is small (21,978 km^2).

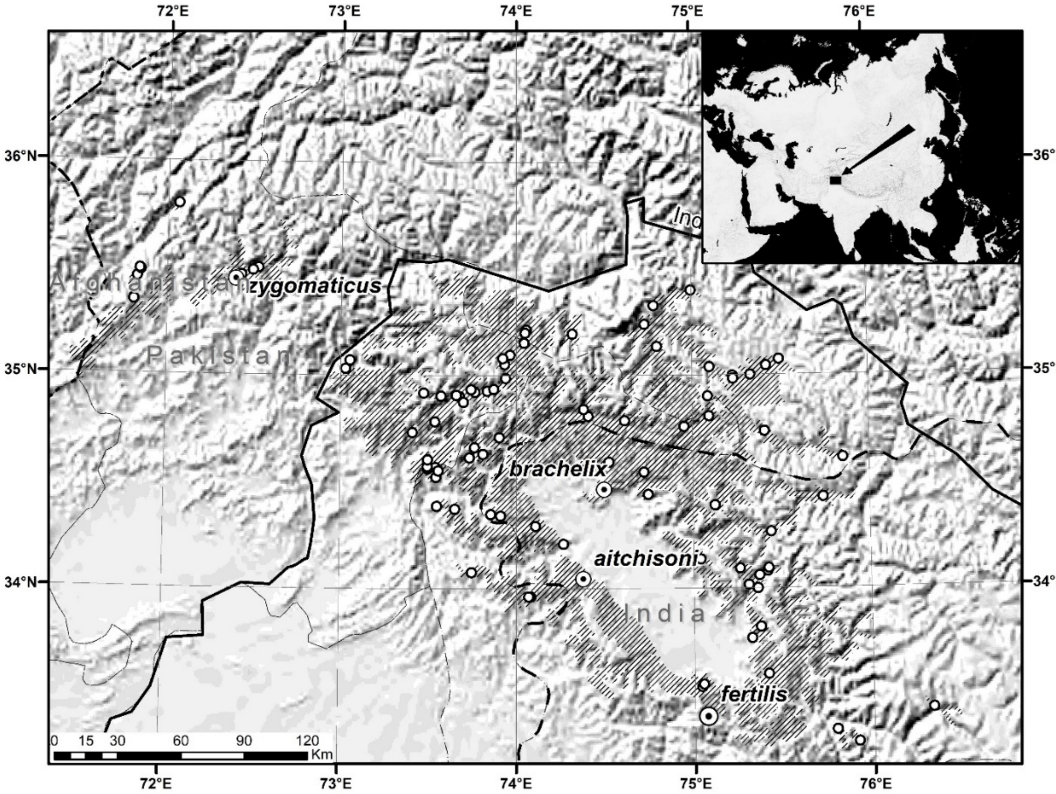


Figure 151: Distributional range of True's Kashmir vole *Hyperacrius fertilis*.

Characteristics. Smaller than *wynnei* with a shorter tail (TL/H&B=0.22–0.30) and relatively longer ears. Fur is shorter but soft and velvet-like. Dorsal pelage is dull brown, occasionally shaded buff across the shoulders; flanks are greyer and the belly is dull ochraceous. Tail is obscurely bi-coloured, grey-brown above, dirty whitish below; feet are grey-brown to almost black. Proximal baculum is longer and narrower than in *wynnei* (length=2.5 mm, width=1.5 mm) with weak basal tuberosities (Phillips 1969). For skull and molars see under *wynnei*.

Variation and subspecies. Phillips (1969) recognised 3 subspecies.

Hyperacrius fertilis fertilis (True, 1894)

Arvicola fertilis True, 1894b:10. Type locality: "Pir Panjal range […] 8,500 feet [2,600 m]", Kashmir, Pakistan. The exact location of the type specimen is not known (Phillips 1969).

Synonyms. *Microtus aitchisoni* Miller, 1897.

Distribution. Restricted to the Pir Panjal Mts. (altitude=2,450–2,750 m) of the lower Himalayas in Pakistan. Biogeographic barriers (Jhelum River Plain, the Vale of Kashmir, and the Kashmir River) isolate the nominal subspecies from the main range of *fertilis* (Phillips 1969).

Characteristics. The largest subspecies: HTL=138–144 mm (H&B=91–114 mm), TL=19–38 mm, HF=14–19 mm, EL=8–14 mm, OnL=24.2–25.3 mm, ZgW=15.4–16.4 mm, MxT=5.4–6.4 mm. Upper parts dark brown to black, belly light ochraceous-buff. Interorbital ridge long, interparietal rectangular or slightly triangular; incisive foramina broad.

Hyperacrius fertilis brachelix (Miller, 1899)

Microtus brachelix Miller, 1899a:290. Type locality: "Nagmarg, Kashmir (altitude, 9,000 feet [2,745 m])", Pakistan.

Distribution. High elevations (2,000–3,800m) between the Kaghan Valley (Mansehra District, Pakistan) and Khistwar (Jammu and Kashmir, India).

Characteristics. The smallest subspecies: HTL=127–144 mm (H&B=87–105 mm), TL=19–34 mm, HF=14–19 mm, EL=8–14 mm, OnL=22.7–24.4 mm, ZgW=13.9–15.7 mm, MxT=5.5–6.4 mm. Upper parts dark brown to orange-brown; belly light ochraceous-buff. Supraorbital ridges moderate; interparietal usually triangular; incisive foramina narrow. Voles from the north are brown and those from the south are brighter and smaller (Phillips 1969).

Hyperacrius fertilis zygomaticus Phillips, 1969

Hyperacrius fertilis zygomaticus Phillips, 1969:469. Type locality: "6 mi[les] [9.7 km] SW [south-west of] Utror, 8900 ft [2,710 m], Swat, West Pakistan."

Distribution. North-western part of the range in the Dir District (Khyber Pakhtunkhwa, Pakistan). Altitudinal range=2,700–3,000 m.

Characteristics. Size as in *brachelix*: HTL=126–140 mm, TL=30–35 mm, HF=17–19 mm, EL=8–11 mm, OnL=23.3–24.8 mm, ZgW=15.0–16.8 mm (Philllips 1969). Pelage is brown above, more ochraceous on the sides, cinnamon-buff below. Supraorbital ridges moderate; interparietal usually triangular; incisive foramina narrow; braincase broader and zygomatic arches more expanded.

SUBTRIBE:
Arvicolina Gray, 1821

Arvicolidae Gray, 1821:303. Type genus by tautonomy is *Arvicola* Lacépède.

Arvicolina contains a single genus (*Arvicola*) which is traditionally classified as a close relative to *Microtus* (Musser & Carleton 2005); some authors have synonymised the two genera (e.g. Miller 1896, Heptner 1952). Molecular phylogenetics, on the other hand, retrieved the isolated position of *Arvicola* within the tribe Arvicolini (Buzan et al. 2008, Steppan & Schenk 2017) which revived earlier ideas of separating Microtina and Arvicolina as distinct subtribes (e.g. Kretzoi 1955, Chaline 1975).

GENUS: *Arvicola* Lacépède, 1799 – Water Voles

Arvicola Lacépède, 1799:10. Type species by monotypy: *Mus amphibius* Linnæus.

Synonyms. *Hemiotomys* Sélys, 1836**;** *Paludicola* J. H. Blasius, 1857 (antedated by Wagler 1830 and Hodgson, 1837, for Lissamphibia and Aves, respectively); *Praticola* Fatio, 1867 (antedated in ornithology by Kaup, 1829, and Swainson, 1837); *Ochetomys* Fitzinger, 1867.

Taxonomy. Trouessart (1910) defined the taxonomic scope of *Arvicola* as it is used now. Previously the name was used to accommodate a wide range of voles which are now in different genera and tribes. Miller (1896:69) additionally noted that "numerous species and subspecies are probably confused under the name *'Arvicola amphibius'*". The number of water vole species remained in a state of confusion for the next hundred years and varied between 1 species (Ellerman & Morrison-Scott 1951) and 7 species (Miller 1912a); the majority of authors, however, settled on 3–4 species. Our taxonomy largely follows Mahmoudi et al. (2019).

Distribution. Palaearctic genus, ranging from the Atlantic coast of continental Europe and the west coast of England, Scotland and Wales in the west until Sakha (the Lena and Aldan Rivers) and Xinjiang in the east, and from the shores of the Arctic Ocean as far south as the Mediterranean and Caspian coasts, and Central Asia.

Characteristics (Figure 152). Large and sturdy voles with a short neck, large head and rounded and blunt muzzle. The tail is comparatively long (TL/H&B≈0.5), cylindrical and slightly tapered. It is densely clad with hairs which nearly conceal the annulation and terminate in a slight pencil (length≈4–11 mm). The semi-circular ears barely protrude above the fur; they are thinly clad with rather long hairs. The eyes are small; the rhinarium is small and naked. The feet are broad and slightly fringed by longer white hairs along the external margin of the hands and feet and along both sides of each digit. The toes are equipped with powerful claws; a distinct claw is also present on the thumb. There are 5 (rarely 6) plantar pads which are evidently in the process of reduction. Soles are mostly naked (Figure 153). Dense and long fur (length=8–17 mm) is interspersed with longer black-tipped protruding hairs which are 4–14 mm longer; the underfur is thick and woolly. Colour is highly variable but the majority of water voles are brown, duller along the spine and lighter on the face and flanks; the chest and belly are whitish, light grey or slate-grey and frequently shaded buff. Postero-lateral glands (size=17×12 mm) lie in the lateral position in the region of the first lumbar vertebrae (=flank glands; Stoddart 1971). Females have 8 nipples. The sperm head is falciform (Retzius 1909).

The skull is large and robust with prominent ridges. The occipital tends to be obliquely truncated and the nasals are short, hence the surface of the upper incisors and the occipital condyles are seen in the dorsal view. The

Figure 152: Representatives of water voles: a,b–*Arvicola amphibius* from the Czech Republic; c–*A. persicus* from Hamadan, Iran. Photo: Miloš Anděra (a,b) and Boris Kryštufek (c).

incisive foramens are usually short and narrow, the auditory bullae are relatively small and the basioccipital is wide. The mandible has a prominent masseteric ridge and a deep masseteric fossa on the labial side of the ramus. The alveolar process is conspicuous in fossorial water voles (Figure 154). The upper incisors are either orthodont or proodont. The molars are large and heavy but do not differ greatly from *Microtus*; the re-entrant angles are filled with cement. The salient angles are sharp or round. Namely, the alteration in an angle at which the plane of wear cuts the prism can produce very different patterns from one and the same tooth (Hinton 1926a). The anteroconid complex of M$_1$ has two triangles (T4–T5) which are confluent with the anterior cap; re-entrant angles LR4 and BR3 are frequently obtuse. M^3 has 2 re-entrant angles on each side and a short posterior cap. In the majority of individuals, triangles T2–T3 alternate and T4 widely communicates with the cap. Depending on the species the enamel is either of the archaic type with a thick convex (trailing, lee) band; in the advanced type, enamel on the concave (leading, luv) side is thinner by 20% than on the convex side (Figure 155). Palaeontologists quantify the relative enamel thickness by using the so-called enamel differentiation quotient (SDQ), which is a quotient of enamel thickness on the lee side with the thickness on the luv side as the denominator (cf. Maul et al. 2020). Young water voles do not show the final differentiation between the two enamel edges (Kratochvíl 1980). On the convex side, the inner enamel is of the lamellar type and is superimposed by radial enamel; on the concave side, the inner lamellar enamel is overlaid by tangential enamel. The reduction of enamel on the convex side is at the expense of the tangential layer which is nearly entirely absent in the advanced stage of enamel differentiation (Koenigswald 1980).

Basal species of water voles (*sapidus, persicus*) are exclusively semi-aquatic just as their presumed ancestors from the extinct genus *Mimomys*. Terminal species (*amphibius* and *italicus*) show habitat-dependent morphological plasticity with two major eco-morphological types, the semi-aquatic and fossorial (Mahnmoudi et al. 2019).

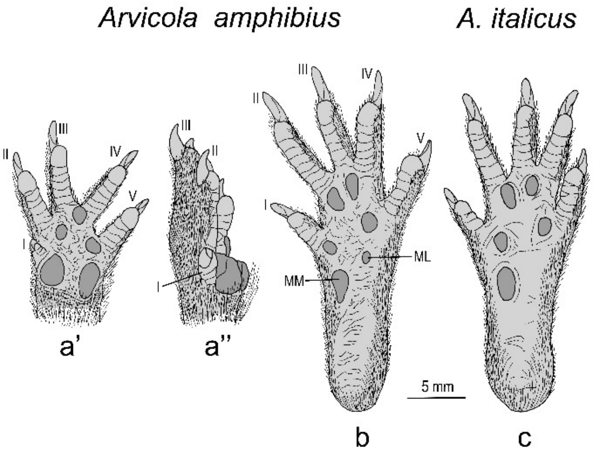


Figure 153: Left palm (a'–ventral, a"–lateral views) and sole (b,c) in water voles: a–*Arvicola amphibius* (central Slovenia); b–*A. amphibius* (western Germany); c–*A. italicus* (Calabria, Italy). Note the tiny 6th metatarsal pad (ML) in inset b.

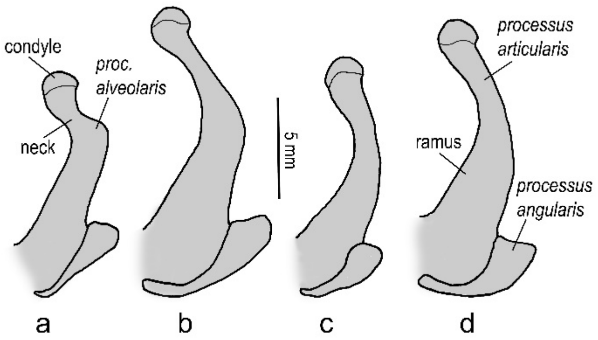


Figure 154: Caudal view of the left ramus mandibulae in fossorial (a) and semi-aquatic (b) *Arvicola amphibius* (from northern Spain and Scotland, respectively); c–*A. italicus* (Pisa, Italy); d–*A. sapidus* (Salamanca, Spain).

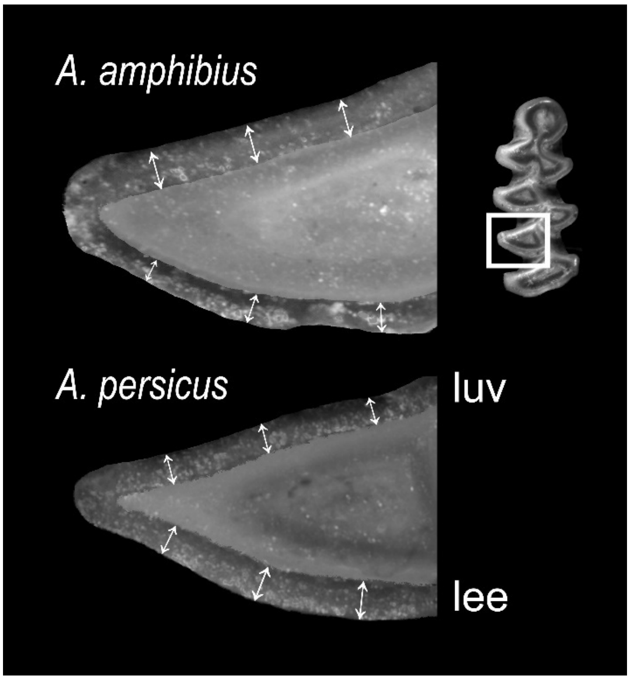


Figure 155: The leading (luv) and the trailing (lee) enamel edges of postero-lingual triangle T1 on first lower molar M_1 in *Arvicola amphibius* (top; from Slovenia) and *A. persicus* (bottom; Iran). Up-down arrows are set at 3 positions to measure the enamel thickness used to calculate the standard difference quotient (SDQ). The SDQ is usually defined as an average of scores obtained at three points per leading and trailing edges, respectively.

Key to species

1a) 2n=40; baculum with a deep notch on the posterior margin of its basal expansion; central distal baculum does not ossify ……………………................... *sapidus*
1b) 2n=36; basal expansion of the baculum without a notch; central distal baculum ossified …….………. 2
2a) Present in Italy and adjacent regions; enamel band is of similar thickness on the lee and luv sides (mean SDQ=90–110 in both the upper and lower molars) ……………………………………………….... *italicus*
2b) Absent from Italy; enamel band differs in thickness between the lee and luv sides ……………………….. 3
3a) Length-to-width ratio of the proximal baculum >1.5; differentiation of enamel is positive (the luv band is thicker than the lee band)…………………...... *amphibius*
3b) Length-to-width ratio of the proximal baculum <1.5; differentiation of enamel is negative (the luv band is thinner than the lee band).. …………………...... *persicus*

Arvicola sapidus Miller, 1908 – Iberian Water Vole

Taxonomy. In the past *Arvicola sapidus* was believed to be most closely related to *amphibius* of Great Britain (Miller 1912a, Barrett-Hamilton 1914) and was frequently synonymised with it (Cantuel 1943, Didier 1943, Niethammer 1956, Brink 1968). The species status of *sapidus,* as proposed by Miller (1908b), was supported by chromosomal and morphological evidence (Heim de Balsac & Guislain 1955, Matthey 1955, Corbet et al. 1970) and is now generally accepted. The species is possibly in a sister position against *amphibius+italicus* sharing TMRCA at 1.535 Mya (Mahmoudi et al. 2019); Centeno-Cuadros et al. (2009b) estimated the time of divergence between *sapidus* and the remaining water voles at 252 kya.

Distribution (Figure 156). All of France as far north as the English Channel and the 50th northern parallel; the eastern border tentatively follows the 5th meridian, also encompassing the Provence–Côte d'Azur in the south. Present throughout the Pyrenees (including Andora), Portugal and the majority of Spain except for the arid central and southern parts (Castile and Leon, Extremadura, southern Castile La Mancha, and Almeria). The entire range covers an estimated 964,860 km^2. Altitudinal range is from sea level up to 2.825 m, but the majority of sites are below 1,000 m. The Iberian water vole is strictly semi-aquatic, occupying the shores of streams, ditches, ponds and canals with dense, tall and lush plant cover; also present in reed-beds, marshland, and brackish water. In part of its range, *A. sapidus* is sympatric with the fossorial *A. amphibius* (Ventura 2012).

Characteristics. Strictly semi-aquatic water voles with orthodont incisors and a long tail (TL/H&B=0.55–0.67). Dorsal pelage is ochraceous-brown, sprinkled in the mid-dorsal region with black-tipped hairs; face and flanks are lightest and frequently shaded buffy. The belly is a various mixture of drab-buff and slate hair bases. Summer pelage tends to be more reddish. Feet are drab-grey and tail is brownish, lighter below. The skull is large and robust with moderately expanded zygomatic arches

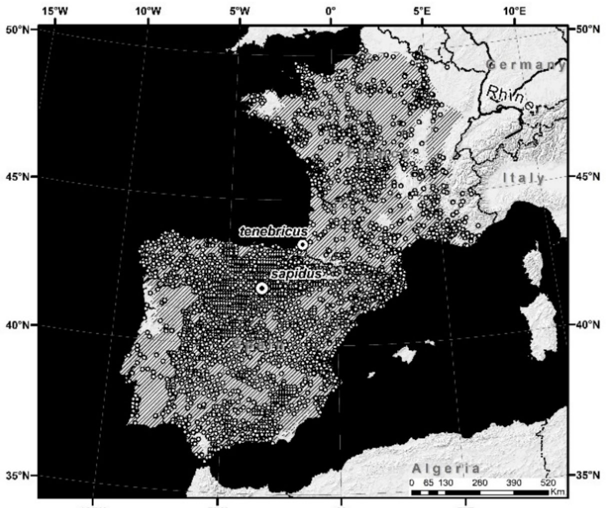


Figure 156: Distributional range of the Iberian water vole *Arvicola sapidus*.

(ZgW/CbL=0.56–0.62) and prominent ridges (Figure 157). In comparison with *amphibius* of comparable size, *sapidus* has wider nasals (range=4.6–6.4 mm *v* 3.8–5.4 mm in *amphibius*) and longer incisive foramina (6.7–8.7 mm *v* 5.1–7.9 mm); *sapidus* also tends towards less expanded zygomatic arches and a comparatively longer and shallower braincase (Reichstein 1963). Grinding surface of molars is essentially as in *amphibius*. Of the anterior re-entrant angles on M_1, the lingual LR4 tends to be more acute than the buccal BR3 which gives the anterior cap an asymmetric appearance; in *amphibius* the two re-entrant angles are usually equally deep which results in a more symmetric anterior cap (Paunesco & Brunet-Lecomte 2013) (Figure 158b). The luv enamel band is thinner (thickness on M_1=57–65µm) than the lee band (68–78µm); SDQ≈120 for M_1 and 83–84 for M^3 (Röttger 1987). Baculum is robust (length-to-width ratio=1.14–1.50). Distal trident is usually cartilaginous; the central distal digit is shorter than the lateral processes which on rare occasions show small ossification centres. The proximal bone (length=3.9–5.4 mm) has an expanded base (width=3.3–4.68 mm) with a deep notch on its posterior margin (Figure 159a). The baculum in juveniles has similar proportions to *amphibius* but the posterior margin already shows a prominent notch (Didier 1943, 1954, Heim de Balsac & Guislain 1955; Rey Salgado 1976). Karyotype: 2n=40, NF_a=64; the X chromosome is bi-armed and the Y chromosome is small acrocentric (Matthey 1955).

Variation and subspecies. Two subspecies are usually distinguished on the basis of colour differences (Miller 1912a, Pardiñas et al. 2017) but were not supported in phylogenetic analysis (Centeno-Cuadros et al. 2009a).

Arvicola sapidus sapidus Miller, 1908

Arvicola sapidus Miller, 1908b:195. Type locality: "Santo Domingo de Silos, Province of Burgos, Spain".

Distribution. Spain, Portugal and southern France (Aude, Camargue and the Alps).

Characteristics. Fur is lighter with yellowish brown flanks and face. Dimensions: BWt=140–327 g, H&B=170–233 mm, TL=97–147 mm, HF=31–39 mm, EL=17–19 mm, CbL=39.0–44.4 mm, ZgW=22.1–26.8 mm, MxT=9.3–11.8 mm.

Arvicola sapidus tenebricus Miller, 1908

Arvicola tenebricus Miller, 1908b:196. Type locality: "three miles [4.8km] east of Biarritz, Basses Pyrénées, France".

Distribution. Western, south-western (with Massif Central), central and northern France; the Pyrenees and northern and north-western Spain.

Characteristics. Fur is darker due to a more extensive terminal dark band on the hairs; light portions of the fur are more distinctly brown and the shade is less buff; feet and dorsal tail are darker and the flanks and face are lined with black-tipped hairs. Dimensions: BWt=100–275 g, H&B=165–220 mm, TL=105–135 mm, HF=31–38 mm, EL=12–20.4 mm, CbL=36.5–44.6 mm, ZgW=21.6–27.9 mm, MxT=8.7–11.1 mm.

Arvicola persicus Filippi, 1865 – Persian Water Vole

Arvicola amphibius var. *persica* Filippi, 1865:344. Type locality by subsequent designation (Thomas 1907b:201): "Sultanieh, … on the plateau south of the Elburz [Mts.]", northern Iran.

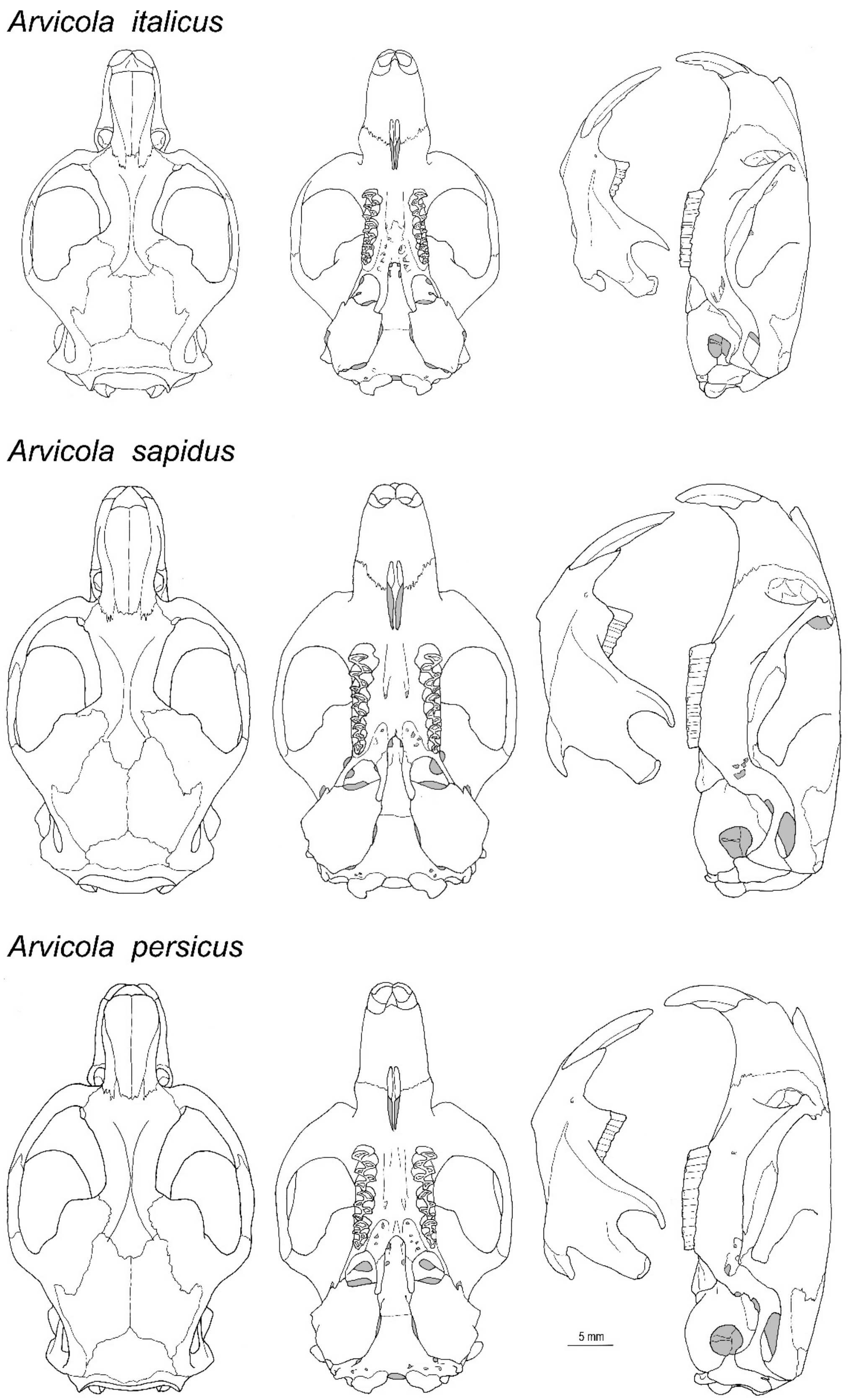


Figure 157: Skull in water voles (top to bottom): *Arvicola italicus* (southern Switzerland), *A. sapidus* (Linares de Riofrío, Salamanca, Spain), and *A. persicus* (Hamadan, Iran).

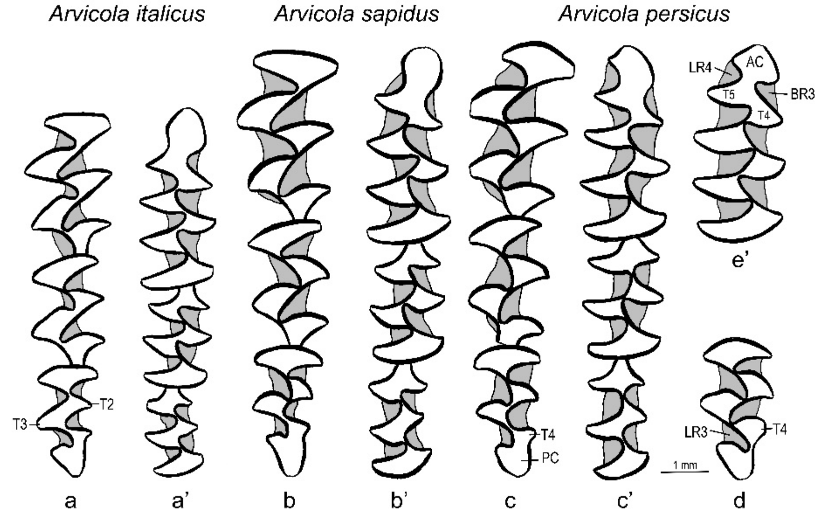


Figure 158: Grinding molar pattern in water voles. *Arvicola italicus*: upper (a) and lower row (a'; Camigliatello, Calabria, Italy). *A. sapidus*: upper (b) and lower row (b'; Linares de Riofrío, Salamanca, Spain). *A. persicus*: upper (c) and lower row (c'; Marand, Azerbaijan, north-western Iran); isolated M^3 (c) and M_1 (d'; Aggel', Azerbaijan).

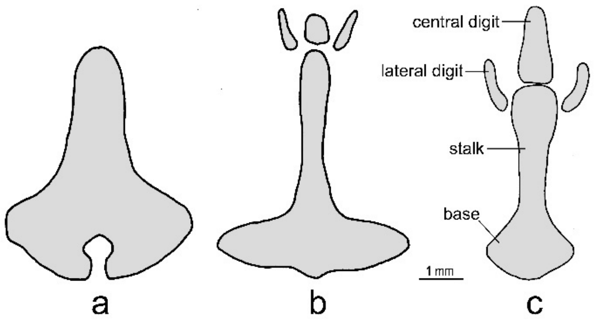


Figure 159: Shape of baculum in water voles: a–*Arvicola sapidus* (France), b–*A. persicus* (Hamadan, Iran), c–fossorial *A. amphibius* (Slovenia).

Synonyms. *N*[*esokia*] *argyropus* Cabrera, 1901; *Microtus terrestris armenius* Thomas, 1907.

Taxonomy. *Arvicola persicus* was synonymised with *terrestris* [=*amphibius*] by Thomas (1907b) and consistently treated this way until Mahmoudi et al. (2019) demonstrated its status as an independent species. The Persian water vole holds a basal position in the genus and presumably diverged in the Early Pleistocene (2.545Mya; Mahmoudi et al. 2019). Its taxonomic and geographic scope is still not firmly defined. Extant populations from Central Anatolia, Hatay and Israel have M_1 SDQ>1 (Maul et al. 2020), i.e. within the range of *persicus,* but water voles from Konya have *Cytb* makeup of *amphibius* (Kryštufek et al. 2015a). We tentatively retain these populations, along with the type of *hintoni*, in the scope of *amphibius*; *armenius* was synonymised with *persicus* as far back as by Hinton (1926a:408).

Distribution (Figure 160). Mountainous regions (altitudinal range=975–2,625 m) of western Iran (Chahar Mahall va Bakhtiari, Esfahan, Hamadan, Kerhmanshahan, Kordestan, Lorestan, Mezandaran, Tehran, West Azarbaijan, Zanjan), Azerbaijan, Armenia, eastern Turkey (east of the River Euphrates) and likely Georgia; a single record is known from Iraq (As-Sulaymaniyah). Distributional area is estimated at 379,370 km². Altitudinal range is from sea level (at the Caspian Sea shore from –23 m) up to 2,800 m. This is a strictly semi-aquatic species, occupying densely vegetated banks of rivers, streams, ponds, lakes and irrigation ditches. Lay (1967) noted that the eastern limit of the range coincides with the western limit of a murine *Nesokia indica* in Iran, attributing this to competitive exclusion.

Characteristics (Figure 152c). Externally and cranially similar to other large semi-aquatic water voles (*amphibius* and *sapidus*) though the tail is comparatively longer (TL/H&B=0.56–0.80). Dimensions: BWt=115–176 g, H&B=145–223 mm, TL=100–139 mm, HF=29–37 mm, EL=12.3–21 mm, CbL=35.3–44.3 mm, ZgW=19.7–25.4 mm, MxT=8.7–11.6 mm. Dorsal pelage varies from buffy-brown to dark greyish brown with a strong admixture of black, especially along the

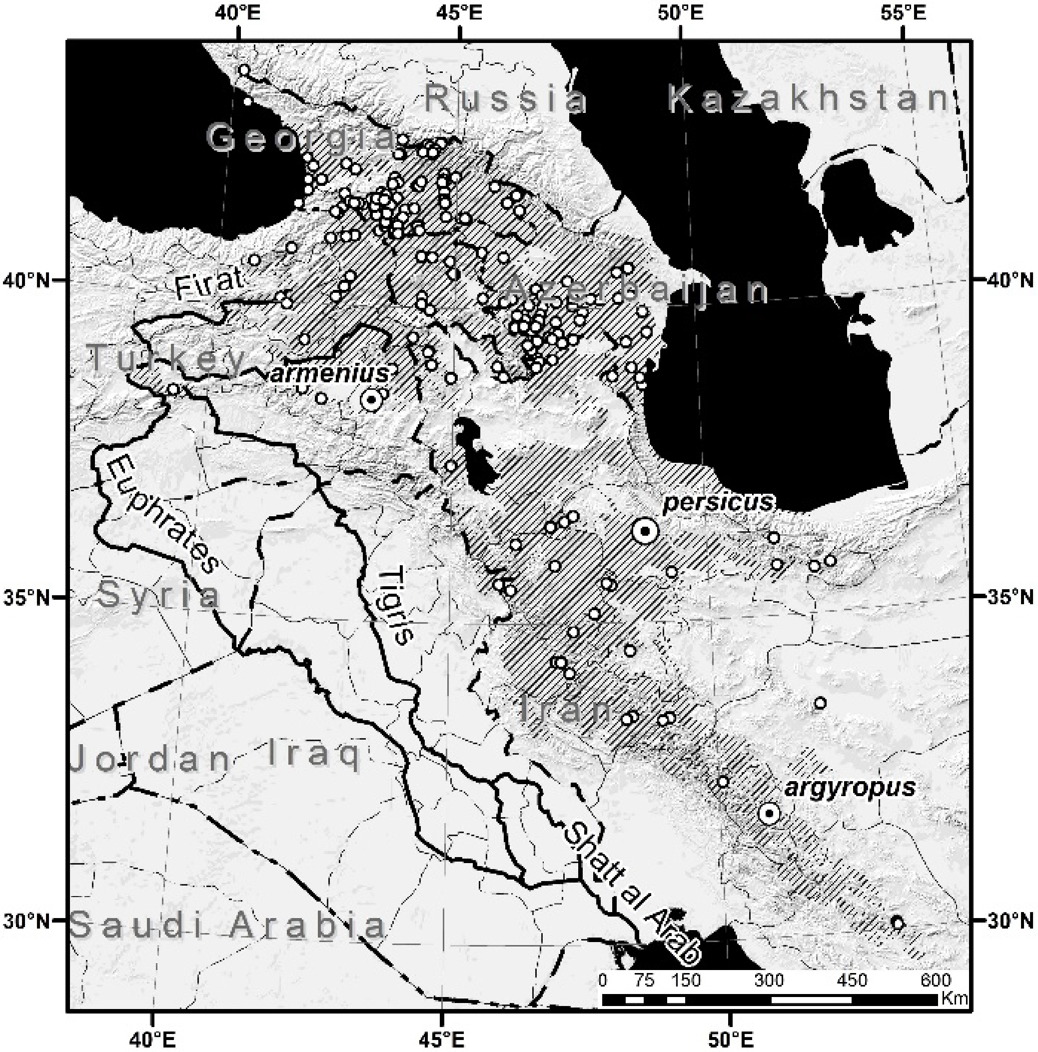


Figure 160: Distributional range of the Persian water vole *Arvicola persicus*.

spine; flanks are considerably lighter, buffy or rusty. Underside is whitish grey and clearly demarcated from the flanks. Mid-dorsal hairs measure 11–12 mm and the sparse protruding black-tipped hairs are longer by ~10 mm. The tail is bi-coloured or has a narrow medial streak of brownish hairs; it is clothed with scanty hairs which terminate in a pencil (length=9.5 mm). Hands and feet are silvery or light yellowish-cream. Skull is as in *amphibius* (Figure 157); zygomatic arches are moderately expanded (ZgW/CbL=0.55–0.60) and the nasals are anteriorly widened. The overall dental pattern shows no peculiarities but the enamel is negatively differentiated (Figure 155), i.e. with a thick trailing band on M_1 (mean SDQ in two populations was 124.3 and 134.4) and a thick leading band on M_3 (SDQ=75.8 and 67.5; Röttger 1987). Proximal baculum (length=5.0 mm, width=4.4 mm) is of similar proportions as in *sapidus* (length-to-width ratio =1.2) but differs by an abruptly expanded base which is antero-posteriorly narrowed. The distal baculum is small; the lateral baculum is 0.8 mm long while the globular central digits measures 0.6×0.44 mm (Figure 159b). Conventional karyotype (2n=36, NF_a=60) does not differ from that of *amphibius*; differential staining (C-banding) retrieved a higher number of NOR-carrying autosomal pairs and acrocentric pairs possessing distinct C-positive bands (Şeker et al. 2018).

Variation and subspecies. Monotypic.

Arvicola italicus Savi, 1838 – Italian Water Vole

Taxonomy. Hinton (1926a) synonymised *italicus* and *musignani* with *terrestris* [=*amphibius*] which until recently has not been challenged. *Arvicola italicus* is a sister species with respect to *amphibius*; TMRCA is estimated at 0.861

Mya (CI=0.572–1.245; Mahmoudi et al. 2019). In comparison to *amphibius*, *italicus* displays a more conservative pattern of enamel differentiation. Morel (1981) demonstrated partial reproductive isolation between *italicus* and the fossorial *amphibius* in Switzerland.

Distribution (Figure 161). Endemic to Italy and also very marginally present in southern Switzerland (Ticino) and western Slovenia. The northern border is set by the Alps and the north-eastern border is delimited by the Dinaric Alps. Our habitat modelling suggested a large-scale fragmentation with a large gap in Basilica, western Puglia and eastern Campania. The area of distribution is estimated at 126,345 km^2; altitudinal range is from sea level up to 1,530 m. Lives in densely vegetated water-banks (also brackish water) and orchards. Available evidence suggests allopatry between *italicus* and the fossorial morphotype of *amphibius* in Switzerland (Fayard 1984) and north-eastern Italy (Lapini & Paolucci 1994).

Characteristics. Moderately large water voles which are externally well within the variation range of *amphibius* though they do not reach the extremes of the fossorial–semi-aquatic continuum. Dimensions: BWt=73–250 g, H&B=163–201 mm, TL=88–102 mm, HF=27.5–29.6 mm, EL=15–16 mm, CbL=36.0–39.0 mm, ZgW=21.6–24.2 mm, MxT=8.8–10.0 mm. Tail is rather short (TL/H&B=0.47–0.57). The pelage is brown, similar to *amphibius* though lighter on average, more yellowish (particularly shoulders and cheeks), and less grizzled with black hair tips. The underside is light slate-grey and heavily washed buff or rusty, particularly on the chest and upper abdomen. Feet are drab to light-brown and tail is obscurely bi-coloured blackish-brown above and grey below. Skull has normally expanded zygomatic arches (ZgW/CbL=0.59–0-63); braincase is shallower

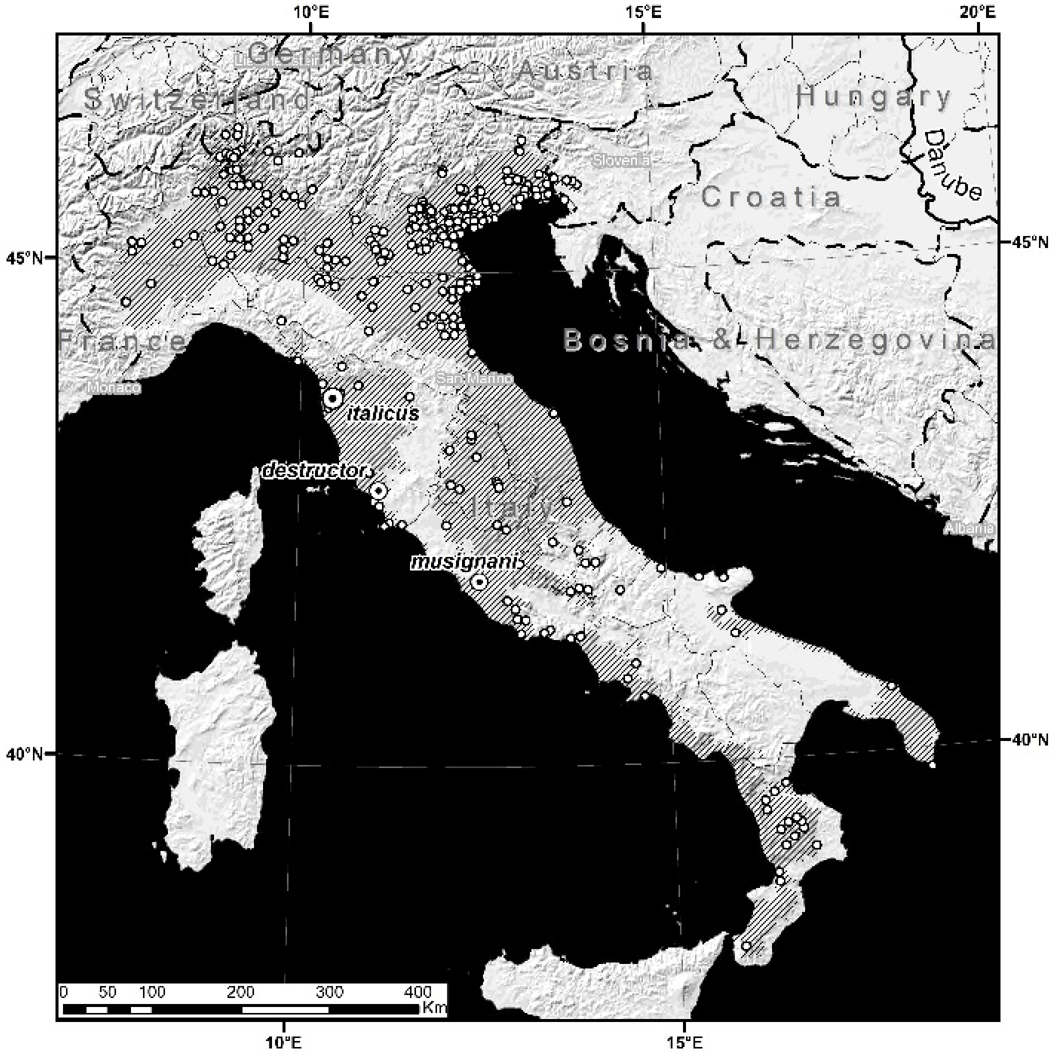


Figure 161: Distributional range of the Italian water vole *Arvicola italicus*.

than in *amphibius* and bullae tend to be smaller (Figure 157); nasals are of variable shape and can widen anteriorly. Mandible has no peculiarities; the alveolar process on the outer side of the mandibular ramus is barely perceptible (Figure 154c). Upper incisors are vertical or slightly proodont; they never protrude like in the extremely fossorial *amphibius*. Molars show a normal grinding pattern (Figure 158a). The trailing and leading enamel bands are of comparable thickness, hence there is not much difference between the SDQ-values scored on the upper or lower molars. Mean SDQ scores in two Italian populations were 107.5 and 94.3 (M^3) and 94.2 and 98.4 (M_1), respectively (Röttger 1987). Conventional karyotype is as in *amphibius*: 2n=36, NF_a=60 (Castiglia et al. 2016).

Variation and subspecies. *Mt*-phylogeny retrieved two divergent lineages, the Northern and the Southern, which share TMRCA at 0.441 Mya (CI=0.254–0.707 Mya; Mahmoudi et al. 2019). Each lineage involves the fossorial and semi-aquatic morphotypes (Castiglia et al. 2016) which are morphologically less divergent than in *amphibius* (cf. Mahmoudi et al. 2019). Two subspecies which were recognised as distinct species in the past (Miller 1912a), putatively coincide with the *Mt*-lineages and also differ in colouration and size. Since Miller (1912a) and Hinton (1926a) classified water voles from Pisa to the nominal subspecies and those from Tuscany (65 km apart) as *musignani* (=*destructor*), the border between the two subspecies supposedly runs at the 43.5th parallel. This area has not yet been screened for molecular markers.

Arvicola italicus italicus Savi, 1838

Arvicola amphibius var. *italicus* Savi, 1838:202. Type locality was restricted to "Vicinity of Pisa, Italy" (Miller 1912a:740).

Synonyms. *Arvicola Pertinax* Savi, 1838.

Nomenclature. The year of publishing *italicus* is usually cited as 1839 (Ellerman & Morrison-Scott 1951:678, Musser & Carleton 2005:964). Savi's paper was a letter to D. Carlo Passerini dated 5 February 1838, and was issued in volume 36 of the *Nuovo giornale* with 1838 on the cover page. In a bibliographic list entitled *Opere pubblicate e lasciate dal Senatore Prof. Paoli Savi* and attached as an unpaginated appendix to the collection of papers dedicated to Savi in the year of his death in 1871 (*Ala memoria di Paolo Savi. FF Nistri, Pisa.* No editor), 1838 is quoted as the year of issuing of "*Sopra le due grosse specie di Arvicole* …".

Distribution. Northern Italy and adjacent Switzerland.

Characteristics. Characterised by *Mt*-nucleotide sequence. Size large (mean CbL=38.2 mm); dorsal pelage brown and more strongly grizzled by black hair tips; feet light-brown.

Arvicola italicus destructor Savi, 1838

Arvicola destructor Savi, 1838:204. Type locality restricted to "Maremma Grossetana, Tuscany, Italy" (Miller 1912a:744).

Synonyms. *Arvicola musignani* Selys, 1839.

Nomenclature. This subspecies is widely known as *musignani*. As shown above (the nomenclatural section under *italicus*), Savi's *destructor* was published in 1838 (not in 1839) and therefore predates Selys' name from 1839. Synonymy of *destructor* and *musignani* is postulated as far back as Miller (1912a:744).

Distribution. Central and southern Italy.

Characteristics. Characterised by *Mt*-nucleotide sequence. Size small (mean CbL=32.6 mm); dorsal pelage light yellowish-brown, only fainly grizzled by black hair tips; feet light-drab.

Arvicola amphibius (Linnæus, 1758) – Eurasian Water Vole

Mus amphibius Linnæus, 1758:61. Type locality was restricted to "England" (Thomas 1911c:147).

Synonyms. *Mus terrestris* Linnæus, 1758; *Mus paludosus* Linnæus, 1771; *[Mus amphibius]* δ. *ater* J. F. Gmelin, 1788; *[Mus amphibius]* ε. *maculatus* J. F. Gmelin, 1788; *[Mus paludosus] Shermann* Bechstein, 1801; *M.[us] amph.[ibius]*

albus Bechstein, 1801; *M.[us] amph.[ibius] canus* Bechstein, 1801; *M.[us] amph.[ibius] niger* Bechstein, 1801; *M.[us] amph.[ibius] maculatus* Bechstein, 1801; *Mus scherman* Shaw, 1801; *Mus amphibus niger* Sonnini, 1816; *Mus amphibus maculatus* Sonnini, 1816 [preoccupied]; *Lemmus aquaticus* M. Geoffroy & Gerardin, 1817; *Lemmus schermaus* M. Geoffroy & Gerardin, 1817; *Arvicola argentoratensis* Desmarest, 1822; *[Hypudæus] [paludosus]* Var. γ. *aq*uaticus Billberg, 1827; *[Hypudæus] [terrestris]* Var. β. *ater* Billberg, 1827; *[Hypudæus] [paludosus]* Var. β. *littoralis* Billberg, 1827; *Lemmus arvalis β Buffonii* J. B. Fischer, 1829; *Arvicola ater* Macgillivray, 1832 [homonym of *ater* Billberg]; *Arvicola monticola* Selys, 1838; *Arvicola Americana* Gray, 1842; *A.[rvicola] terrestris* Var. *castaneus* Selys, 1845; *[Arvicola terrestris]* var. *niger* Selys, 1845 [nomen nudum]; *A.[rvicola] amphibius* var. *minor* Selys, 1845 [nomen nudum]; *A.[rvicola] amphibius* var. *major* Selys, 1845 [nomen nudum]; *[Arvicola amphibius*] subvar. *nigricans* Selys, 1845 [nomen nudum]; *A.[rvicola] amphibius* Aberr. *albomaculatus* Selys, 1845 [nomen nudum]; *[Arvicola Musignani] fuliginosus* Sélys, 1845 [nomen nudum]; *Ochetomys amphibius, nigro-fuscus* Fitzinger, 1867 [nomen nudum]; *Microtus musignani illyricus* Barrett-Hamilton, 1899; *M.[icrotus?] aquatilis* König-Warthausen, 1875 [nomen nudum]; *Microtus terrestris rufescens* Satunin, 1908; *Arvicola amphibius reta* Miller, 1910 [new name for *ater* Macgillivray]; *Arvicola scherman exitus* Miller, 1910; *Arvicola amphibius pallasii* Ognev, 1913 [nomen nudum]; *Arvicola terrestris scythicus* Thomas, 1914; *Arvicola taurica* Ognev, 1922; *Arvicola amphibius meridionalis* Ognev, 1922 [nomen nudum]; *Arvicola terrestris ognevi* Turov, 1926; *Arvicola terrestris abrukensis* Reinwaldt, 1927; *Arvicola amphibius djukovi* Ognev & Formozov, 1927; *Arvicola amphibius brigantium* Thomas, 1928; *Arvicola amphibius kuruschi* Heptner & Formozoff, 1928; *Arvicola amphibius tanaitica* Kalabuchow & Rajewskij, 1930; *Arvicola terrestris hintoni* B. Aharoni, 1932; *Arvicola terrestris tataricus* Ognev, 1933; *Arvicola terrestris ferrugineus* Ognev, 1933; *Arvicola terrestris meridionalis* Ognev, 1933 [first proper use of *meridionalis* Ognev, 1922]; *Arvicola terrestris volgensis* Ognev, 1933; *Arvicola terrestris caucasicus* Ognev, 1933; *Arvicola terrestris cubanensis* Ognev, 1933; *Arvicola terrestris turovi* Ognev, 1933; *Arvicola terrestris variabilis* Ognev, 1933; *Arvicola terrestris jenissejensis* Ognev, 1933; *Arvicola terrestris kuznetzovi* Ognev, 1933; *Arvicola terrestris jacutensis* Ognev, 1933; *Arvicola terrestris korabensis* V. Martino & E. Martino, 1937; *Arvicola terrestris obensis* Egorin, 1939; *Arvicola terrestris uralensis* Egorin, 1940; *Microtus terrestris barabensis* Heptner, 1948 [new name for *variabilis* Ognev, 1933]; *Microtus terrestris karatshaicus* Heptner, 1948 [new name for *rufescens* Satunin]; *Microtus terrestris hyperryphaeus* Heptner, 1948 [new name for *uralensis* Egorin]; *Arvicola terrestris martinoi* Petrov, 1949; *Arvicola terrestris stankoviči* Petrov, 1949; *Arvicola terrestris černjavskii* Petrov, 1949; *Arvicola terrestris subalpina* Mirić, 1960 [objective synonym of *stankovici* Petrov]; *Arvicola terrestris euskaldunensis* Rey, 1976 [nomen nudum]; *Arvicola terrestris cantabriae* Ventura & Gosálbez, 1989; *Arvicola terrestris gutsulius* Zagorodnjuk, 2001 [nomen nudum].

Taxonomy. Two species of Eurasian water voles were recognised until very recently, the semi-aquatic and widespread *terrestris* (=*amphibius*) and the fossorial *scherman* with a more restricted distribution (Ognev 1950, Panteleyev 2001, Musser & Carleton 2005). *Mt*-DNA phylogenetic reconstruction failed to separate fossorial water voles from their semi-aquatic counterparts (Kryštufek et al. 2015a) and both are reported here as *amphibius*. Fossorial water voles from Switzerland, France, and Spain were classified as a species in its own right (*monticala*) as opposed to *amphibius* which contained the semi-aquatic as well as part of the fossorial populations (including topotypes of *scherman*; Pardiñas et al. 2017). *Mt*-haplotypes of *monticola,* however, are polytopic occurring in south-western Europe and again in Scotland (Piertney et al. 2005) which has caused us to consider *monticola* and *amphibius* as divergent conspecific lineages.

The Eurasian water vole is the most widespread and morphologically variable species in the genus *Arvicola*. It has been suggested that range expansion was facilitated by widening the ecological niche, which in turn was putatively triggered by habitat-dependent morphological plasticity and positive enamel differentiation (Mahmoudi et al. 2019).

Distribution (Figure 162). The extensive distributional range (area=11,573,583 km^2) is largely contiguous between Western Europe and the Ob' River in western Siberia. Further east, water voles are mainly restricted to the Yenisei and Lena Rivers, reaching their easternmost point on the Aldan River (the right tributary of the Lena). The northern border is set by the shores of the

Arctic Sea at latitudes of 70.34 (Norway, Finnmark), 70.63 (Yenisei) and 70.996 (Lena). The southern border follows northern Spain, the Pyrenees, the Alps, Dinaric Alps, northern Greece and Thrace, Central Anatolia, the Levant coast as far south as Israel, the Caucasus, the edge of the desert belt between the Caspian Sea and Lake Balkhash, the Tien Shan Mts. in Kazakhstan and adjacent Xinjiang (China), the Altai Mts. in western Mongolia, the upper reaches of the Yenisei, Lake Baikal, and the middle course of the Aldan River. Recently, the water vole's presence was confirmed in the Amur River (Belogorsk in Russian Federation; B. Sheftel, personal communication) where it was mentioned as early as by Schrenck (1859; see also comments under *Alexandromys fortis*). On the islands, water voles are widespread in Great Britain but occur on very few islands offshore from England (Wight, Anglesey) and Scotland (several islets in the strait Sound of Jura). Insular occurrences elsewhere in Europe are much less common than one would expect for a semi-aquatic rodent. The species occurs on the islands along the coasts of Holland (Texel, Terschelling) and Denmark (Vendsyssel-Thy, Zealand, Fünen, many islets south of Fünen, Fanø, Mandø, Rømø), and in the Baltic Sea (Öland, Saaremaa, Hiumaa, Åland). Water voles are absent from Ireland and all the Mediterranean islands.

Semi-aquatic water voles occupy an identical habitat to *A. sapidus*, i.e. the shores of streams, dikes and ponds with dense plant cover, reed-beds, marshlands, rice fields and peat-bogs but locally inhabit waterside habitats and dry fields indefinitely (Wijngaarden 1954, Southern & Crowcroft 1956, Panteleyev 2001). The fossorial type inhabits grasslands, orchards and certain crops despite the plentiful availability of vacant aquatic habitats. Depending on the season or population density, certain populations alternate between the aquatic and terrestrial habitats. Altitudinal range is from the Caspian Depression (–27 m) until 3,200 m.

Characteristics. Eurasian water voles display high levels of phenotypic variation associated with varied ecologies. Two distinct allopatric forms (also called ecotypes or ecological forms) are usually distinguished: the fossorial and the semi-aquatic. All fossorial populations are short-tailed (TL/H&B=0.33–0.57), have more reduced plantar pads, softer pelage with shorter protruding hairs (length=15.5–21 mm) and are smaller: BWt=47–219 g, H&B=122–183 mm, TL=35–98 mm, HF=20–30 mm, EL=9–18 mm, CbL=28.4–38.4 mm, ZgW=18.3–25.3 mm, MxT=7.7–9.7 mm. Their skull is brachicephalic with more expanded zygomatic arches (ZgW/CbL=0.57–0.67) and pronouncedly proodont upper incisors (Figure 163) which are also less concealed by the lips. Fossorial forms also differ from the semi-aquatic in diet and life history strategy. They are more territorial, monogamous, occupy smaller home ranges and have cyclic

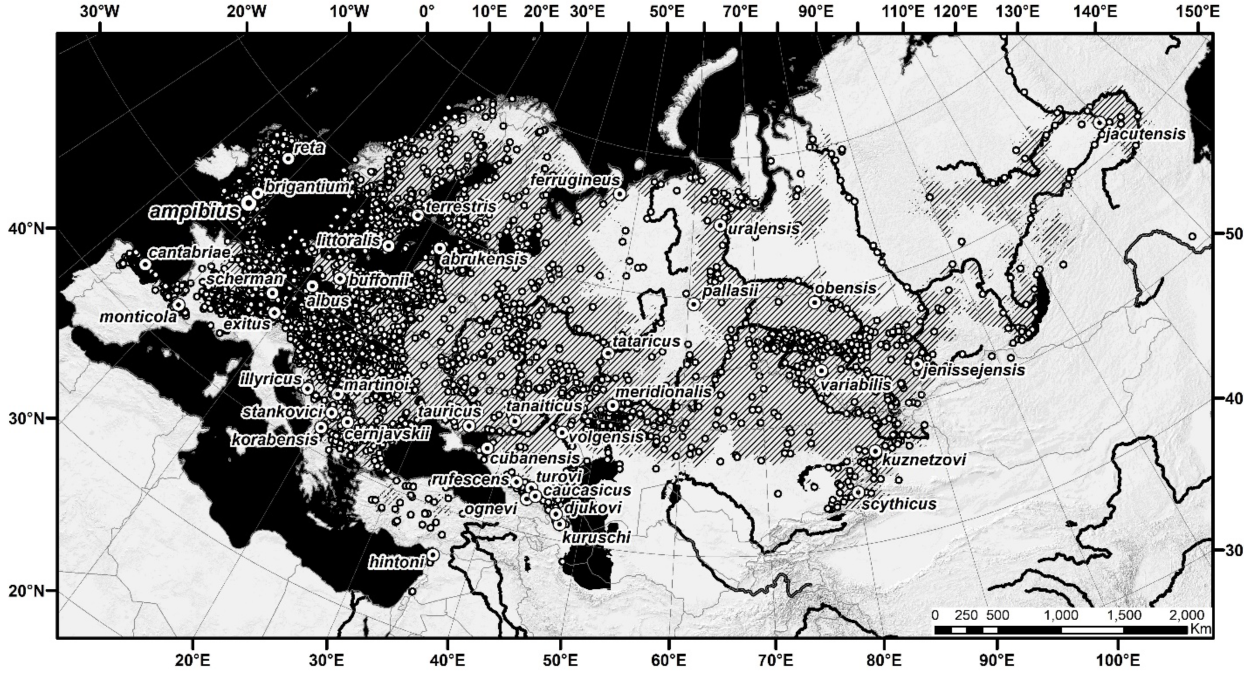


Figure 162: Distributional range of the Eurasian water vole *Arvicola amphibius*.

populations. Semi-aquatic water voles usually have shaggier fur due to more abundant and longer (19.5–28.5 mm) protruding hairs; they display a proportionally longer tail (TL/H&B=0.47–0.77), less reduced plantar pads and are larger: BWt=70–352 g, H&B=121–254 mm, TL=68–150 mm, HF=24–40 mm, EL=10–20 mm, CbL=35.4–44.9 mm, ZgW=20.4–26.9 mm, MxT=8.0–11.4 mm. Zygomatic arches are narrower (ZgW/CbL=0.56–0.64) and orthodont incisors are better covered by the lips. These voles are polygamous, occupy larger home ranges and have more stable populations; only females are territorial. Fossorial morphotype results from heterochronic changes in growth rates (accelerated dwarfism) which affect adult size and shape (Cubo et al. 2006). The differences become apparent early in postnatal life, e.g. in proodonty at the age of 20 days (Kleist 1996). Although the extremes are markedly different, they are nevertheless connected through a gradation of intermediate forms (Corbet et al. 1970, Mahmoudi et al. 2019). E.g. on high-altitude pastures of the Caucasus, water voles are smaller, live away from water and show cyclic population changes (Tembotov 1966) but are still more similar to their semi-aquatic conspecifics from the lowlands than to the truly fossorial water voles of Europe. Cross-breeding of European fossorial and semi-aquatic water voles yielded fertile offspring (Bernard 1961, Kleist 1996).

In the genus *Arvicola*, Eurasian water voles show the most progressive positive enamel differentiation with the luv side ⅓ thicker than the lee side. Glans penis is

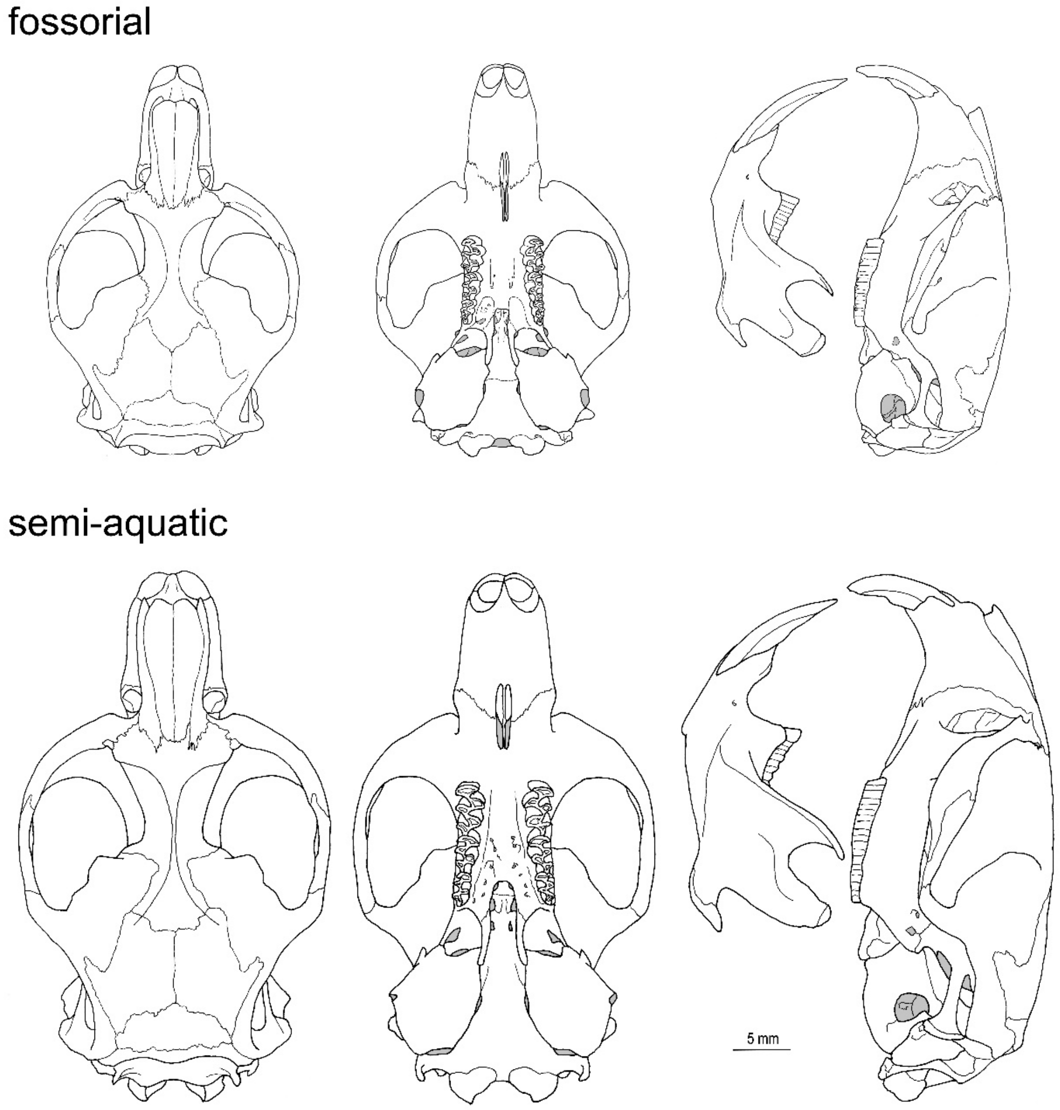


Figure 163: Skull in fossorial (top) and semi-aquatic (bottom) *Arvicola amphibius* from Bassins, Vaud, Switzerland (top) and Edinburgh, Scotland (bottom).

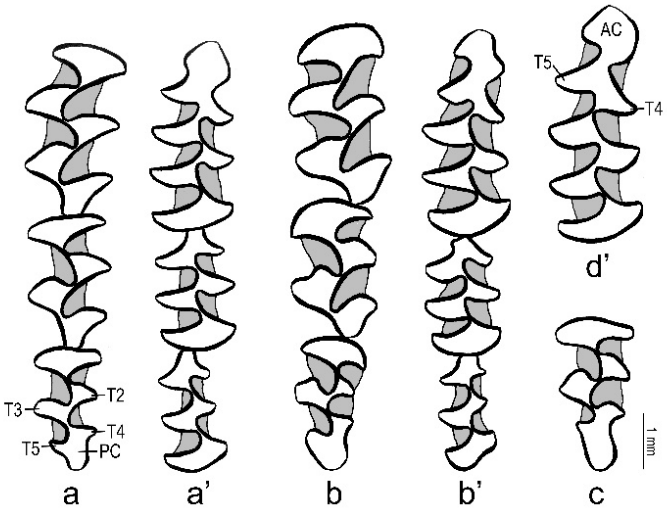


Figure 164: Grinding molar pattern in *Arvicola amphibius*: upper (a) and lower row (a') in the fossorial type from Ribadesella, Asturia, Spain; upper (b) and lower row (b') in a semi-aquatic type from Studenec, Moravia, Czech Republic; isolated M^3 (c; Astrakhan, Russian Federation) and M$_1$ (d'; Edinburgh, Scotland).

club-shaped and covered with tiny spines (Özkurt et al. 1999). Baculum is slightly longer than the glans; the proximal baculum (length=3.4–6.6 mm, basal width=1.2–3.7 mm) has a variable outline of the posterior base (triangular, rounded, straight or slightly concave) but always lacks the deep notch which is obvious in *sapidus*. Length-to-width ratio of the proximal baculum is 1.83–2.72. Ossification is complete in the medial distal digit (length=1.4–2.5 mm) and incomplete in the lateral digits (length=0.8–1.3 mm) (Didier 1954, Heim de Balsac & Guislain 1955, Hooper & Hart 1962, Aksenova 1983). Chromosomes: 2n=36, NF$_a$=60–68; the X chromosome is bi-armed and the Y is acrocentric and usually the same size as the smallest acrocentric pair (Zima & Král 1984). Differences against the karyotype of *sapidus* are putatively the result of Robertsonian translocations and pericentric inversions (Díaz & Pretel 1979).

Variation and subspecies. Eurasian water voles are highly variable in size, relative length of tail, colouration, and cranial shape. They were therefore split into a large number of subspecies (see list of synonyms) with the vast majority being semi-aquatic. Fossorial water voles live contiguously from northern Spain to Central Europe. Although they obviously centre on the European mountain ranges (the Cantabrian Range, the Pyrenees, Massif Central, the Alps and the Carpathians) they also occur at low altitudes. On the other hand, semi-aquatic populations occupy lowlands as well as high elevations. E.g. the Balkan Mountains are exclusively inhabited by semi-aquatic water voles. In some areas (e.g. Holland, Schreuder 1933; the Caucasus, Tembotov 1966), local adaptations lead to the proximity of dissimilar forms or to their patchy distribution. This complexity triggered an excessive taxonomic split; e.g. 7 subspecies are reported from the Caucasus alone. Corbet (1978:105) rightly stressed that the variation in Eurasian water voles "cannot be usefully described by orthodox subspecific taxonomy."

The major divergence is into two phylogenetic lines, the *monticola* lineage from western Europe and Scotland and the *amphibius* lineage in Central and Eastern Europe, Asia and England (Piertney et al. 2005, Brace et al. 2016). Within the *amphibius* lineage, phylogeographic structuring is imperfectly known due to incomplete sampling and reliance on *Mt*-markers. Water voles from Anatolia and Siberia, respectively, seem to be the most distinct (Kryštufek et al. 2015a).

Unusual coat colour has frequently been observed in Eurasian water voles. Partial albinos and all-black or even melanistic water voles were recorded at different frequencies throughout the entire range of the species (Panteleyev 2001). Small partial albinisms are present in three main sites of the body (the tip of the tail, the crown of the head, and the chest). Such animals are frequent in certain populations; e.g. a white crown on the head reaches a frequency of >90% in Scotland and >20% in western Kazakhstan. A white tip of the tail is present in 69% of individuals in Kabardino-Balkaria and in >30% of voles from Scotland, Switzerland, Dagestan, and parts of Kazakhstan (reviewed in Panteleyev 2001). Populations composed of black (blackish-brown or melanistic) individuals usually associate with the semi-aquatic voles and are known from several sites in Great Britain (most notably Scotland) and in several places in Central Europe (e.g. Dinkelland in Holland and Balaton in Hungary).

SUBTRIBE:
Microtina Rhoads, 1895

Microtinæ Rhoads, 1895:940.

Nomenclature. The subfamily name Microtinae is credited to Miller (1896:8) although Rhoads' (1895) naming antedates Miller's by 1 year and therefore holds absolute priority.

Taxonomy. Usually synonymised with Arvicolina; such an arrangement is untenable as Arvicolina is paraphyletic with respect to Microtina. See Arvicolina for further comments. Microtina is the central group of Arvicolinae, containing 59% of all species.

Distribution. The same as in Arvicolini.

Characteristics. Similar to *Arvicola* but smaller on average with a shorter tail and more complex M^3 and M_1.

Key to genera, subgenera and species groups

1a) Whisker long (>30 mm) ………………………… 2
1b) Whiskers shorter (<30 mm) ………………………… 3
2a) 4 nipples; present in Taiwan ………………………… *Alexandromys* (*Yushanomys* n. sgen.)
2b) 8 nipples; present in south-western Palaearctics ………………………… *Chionomys*
3a) Upper incisors are broad 2.4–2.7 mm); molar pattern simple: T4 on M^1 much smaller than T3; M^3 with 4 – 5 closed dental fields, M_1 with 6 closed fields; present in Sichuan and Gansu (China) ………………………… 4
3b) Upper incisor not particularly broad (usually <2 mm); molar pattern frequently complex ………………… 5
4a) Front surface of upper incisors grooved; M^3 with 4 closed fields; short-tailed (TL/H&B>0.5); HF<21 mm; CbL<28 mm; MxT<6.9 mm; cranial dorsal profile is evenly bowed ………………………… *Proedromys*
4b) Front surface of upper incisors smooth; M^3 with 5 closed fields; long-tailed (TL/H&B>0.5); HF>20 mm; CbL>28 mm; MxT>6.8 mm; cranial dorsal profile is flat ………………………… *Mictomicrotus* n. gen.
5a) Medial dark stripe may be present on the back; skull width across zygomatic arches barely exceeds braincase width; ZgW/CbL≤0.56; molars have an elongated appearance ………………………… *Stenocranius*
5b) Medial stripe never present; zygomatic arches obviously wider than the braincase; ZgW/CbL≥0.55; molars of normal appearance ………………… 6
6a) M_1: dental fields T4–T5 confluent ………………… 7
6b) M_1: dental fields T4–T5 alternate ………………… 13
7a) M_1: dental field T5 confluent with AC ………………… 8
7b) M_1: dental field T5 isolated from AC ………………… 11
8a) Fur is dark (blackish) brown; TL/H&B usually >0.50 ………………………… *Volemys*
8b) Fur is brown with buffy or ferruginous shades; TL/H&B usually <0.50 ………………………… 9
9a) Postero-lateral glands are on the flanks………………………… *Neodon* (part)
9b) Postero-lateral glands are on the hips ………………… 10
10a) M3 usually with 2 deep re-entrant angles on the lingual side; 2n=48–58 ………………… *Microtus* (*Blanfordimys*)
10b) M3 with 3–4 deep re-entrant angles on the lingual side; 2n=30–38 ………………… *Alexandromys* (*Oecomicrotus*)
11a) Postero-lateral glands are on the flanks ………………………… *Neodon* (part)
11b) Postero-lateral glands are on the hips ………………… 12
12a) 4–6 nipples; M^1 with 2 inner re-entrant angles ………………………… *Microtus* (*Terricola*)
12b) 8 nipples; M^1 frequently with 3 inner re-entrant angles ………………………… *Microtus* (*Microtus*) *schelkovnikovi*
13a) Postero-lateral glands are on the flanks ………………………… *Neodon* (part)
13b) Postero-lateral glands are on the hips ………………… 14
14a) Pterygoid fossa is of normal size; bony swelling on the lingual side of the ascending ramus absent; mandibular foramen is at the margin of the posterior *incisura mandibulae*; M_1: AC is of deltoid outline; endemic to Spain and Portugal ………………… *Microtus* (*Iberomys*)

14b) Pterygoid fossa is squeezed by the bony swelling on the lingual side of the ascending ramus; mandibular foramen is shifted away from the margin of the posterior *incisura mandibulae* and towards the pterygoid fossa ……………..15
15a) M^3 with 2 lingual re-entrant angles … *Lasiopodomys*
15a) M^3 usually with 3–4 lingual re-entrant angles 16
16a) Bullae and mastoid chambers enlarged ……………………..… *Microtus* (*Microtus*) *socialis* group
16b) Bullae and mastoid chambers are of normal size 17
17a) 5 plantar pads …......................… *Alexandromys* (part)
17b) 6 plantar pads …….......................................… 18
18a) M^2 with T5; hairs at the base of the ear protrude over it; the antihelix is covered by long and fluffy hairs; distal baculum is rudimentary; sex chromosomes are gigantic ………….………………..... *Microtus* (*Euarvicola*)
18b) M^2 without T5; hairs at the base of the ear do not protrude over it; the antihelix is covered by short hairs; distal baculum is normally developed; sex chromosomes are of standard size …….. *Microtus* (*Microtus*) *arvalis* group

GENUS: *Chionomys* Miller, 1908 – Snow Voles

Taxonomy. *Chionomys* was established as a subgenus of *Microtus*. Although elevated to a genus in its own right as early as the 1930s (e.g. Aharoni 1932), this ranking has only been widely accepted since 1980. Monophylly of *Chionomys* is well-supported by various data sets: cranial (Pietsch 1980), dental (Nadachowski 1991), chromosomal (Agadzhanyan & Yatsenko 1984), and genetic (Jaarola et al. 2004, and subsequent studies). The cradle of snow voles is the area of the Caucasus where all recent species still co-occur. In line with biochemical evidence, *Chionomys* emerged >2.4 Mya but the fossils date back to <1 Mya (Chaline & Graaf 1988). The interpretation of the fossil record is complicated by the overlap in M_1 morphotypes with *Alexandromys oeconomus* and other extant and fossil taxa (Nadachowski 1991). Subsequent divergence of *Chionomys* into two subgenera, which is estimated at 1.77 Mya (CI=1.36–2.19 Mya; Yannic et al. 2012), concurs with fossil data

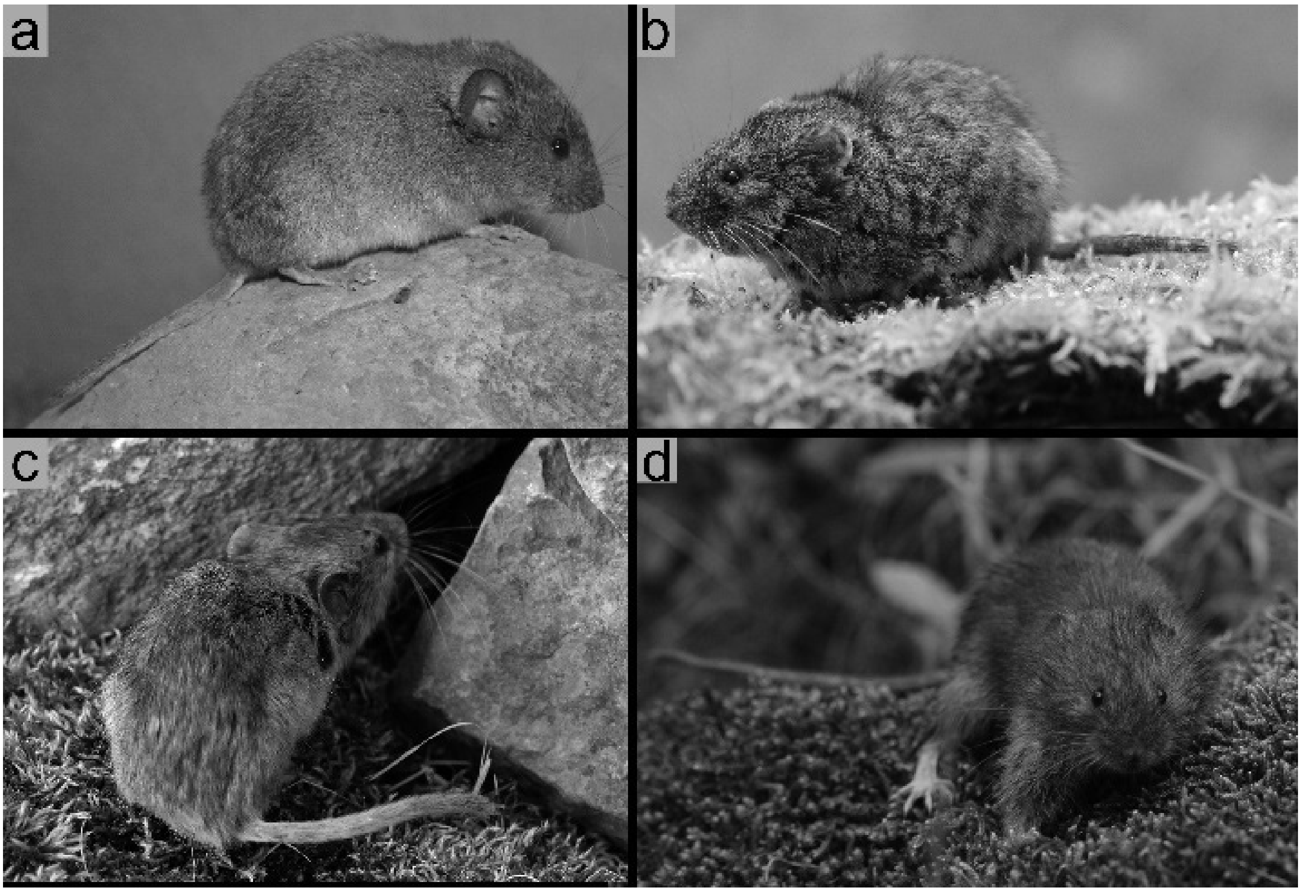


Figure 165: Snow voles (*Chionomys*): a,b–*C. nivalis* (a–As Suwayda, Syria; b–Romanian Carpathians); c–*C. lasistanius* (Turkey); d–*C. roberti* (vicinity of Giresun, Turkey). Photo courtesy: Alenka Kryštufek (a), Gabriel Chişamera (b) and Ahmat Karataş (c,d).

(Nadachowski 1991). This dichotomy was first recognised by Ellerman (1941), who classified snow voles in 2 species groups of *Microtus,* the *nivalis* group (with *C. nivalis*) and the *roberti* group with *C. gud* and *C. roberti.*

Distribution. Mountainous regions of southern and Central Europe and south-western Asia. Three species dwell in rocky fissures and among accumulated outcrops and boulders; the remaining species (*C. roberti*) is presumably semi-arboreal.

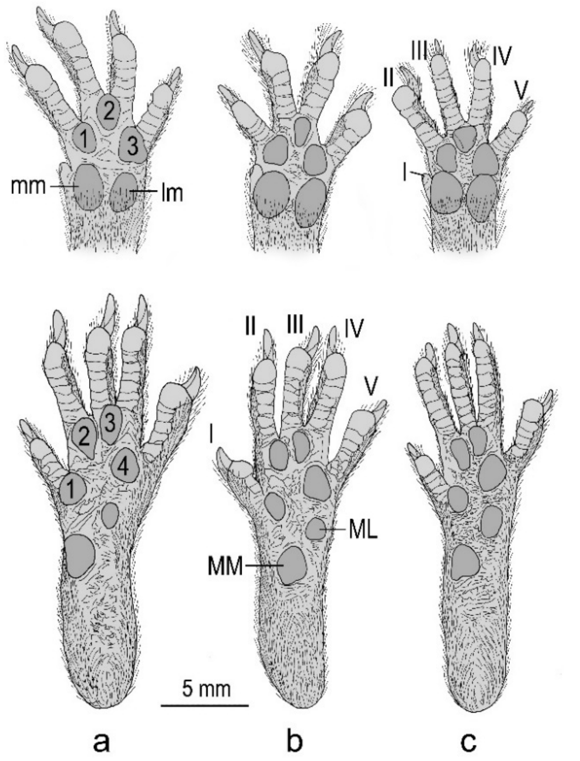


Figure 166: Left palm (top) and sole (bottom) in snow voles (*Chionomys*): a–*C. roberti* (Topçam, Black Sea Mts., Turkey); b–*C. gud* (Gudauri, Greater Caucasus, Georgia); c–*C. nivalis* (Komovi Mts., Montenegro).

Characteristics (Figure 165). Moderately large and long-tailed voles (TL/H&B>0.40) with lengthy mystacial vibrissae and long, soft and dense pelage. The snout is pointed and the ears, which overtop the long fur, are densely clad with short hairs. The tail is covered by stiff hairs which terminate in a weak pencil. There are six large plantar pads; the sole is nude except for the heel (Figure 166). Females have 8 nipples; the distal baculum is frequently not entirely osseous. The skull is relatively narrow (Zg W/CbL=0.54–0.59) and weakly ridged. The interorbital region is broad and flat without a sagittal crest; the braincase is comparatively shallower and also longer than in the majority of Microtina. *Squama carina media* is broad and barely pronounced and the lateral pits on the posterior hard palate are shallow. The mandible is slender with comparatively weak processes; there is no knob (alveolar process) on the outer side of the mandibular ramus. Incisors are orthodont and comparatively weak. With the exception of being weaker, molars are essentially like in *Microtus*; M_1 has a short anteroconid complex (ACC/M_1 length=0.43–0.56). The enamel pattern is as in *Microtus* with scarce tangential enamel on the lee side (Koenigswald 1980). The diploid number is stable (2n=54). The sex chromosomes form a synaptonemal complex during the pachytene stage in both sexes (Megías-Nogaels et al. 2003).

Key to species

1a) Dorsal pelage is dull brown; TL/H&B>0.65 ....*roberti*

1b) Dorsal pelage is greyish or yellowish; TL/H&B<0.65 ……………………..…..................... 2

2a) TL/H&B<0.55; braincase is deep (height across bullae/CbL usually >0.37); bullae larger (length of bulla/CbL>0.27); length of posteroconid complex nearly always <55% of M^3 length, breadth ≤0.60 mm; lateral processes of distal baculum are inconspicuous and frequently cartilaginous; all autosomal chromosomes are acrocentric …………..…...….. *nivalis*

2b) TL/H&B>0.55; braincase is shallow (height across bullae/CbL<0.38); bullae smaller (length of bulla/CbL<0.28); length of posteroconid complex >50% of M^3 length, breadth ≥0.60 mm; lateral processes of distal baculum is large and well-ossified; the smallest autosomal pair is bi-armed ……….……..… 3

3a) Base of baculum with a notch; central digit of distal baculum longer (>1.4 mm); present in the Greater Caucasus (northern Georgia and Russia) …..........…. *gud*

3b) Base of baculum without a notch; central digit of distal baculum shorter (<1.4 mm); present in the Lesser Caucasus (south-western Georgia and Turkey) …………………………………….…..… *lasistanius*

SUBGENUS: *Chionomys* Miller, 1908

Chionomys Miller, 1908a:97. Type species is *Arvicola nivalis* Martins.

Taxonomy. *Chionomys* s.str. contains *C. nivalis* as the only species.

Distribution. Identical to that of the genus.

Characteristics. The subgenus is well-defined by *Mt*-sequences (Yannic et al. 2012, Bannikova et al. 2013). All autosomes are acrocentric. Tail is comparatively short (TL/H&B<0.55) and the lateral metatarsal pad is large (Figure 166c). The distal baculum is incompletely ossified or remains cartilaginous. The skull is deep and the bullae are more swollen than in *Protochionomys* new subgenus (length of bullae/ CbL=0.27–0.38). M^1–M^2 occasionally show constricted base which expands posteriorly (Figure 167b), similar to *M. (Iberomys) cabrerae*; rarely there is also an additional postero-lingual triangle (T5) which opens to T4. M^3 has 3 salient angles on either side in ~80% of cases (Figure 167a), hence the posteroconid complex is short (in nearly all populations <55% of M^3 length; the total range=33–61%; Nadachowski 1991). M_1 shows separated dental fields T5–T6 in >50% of cases and frequently lacks the antero-labial re-entrant angle BR4 (Figure 167a'). Karyotype: all autosomes are acrocentric.

Chionomys nivalis (Martins 1842) – European Snow Vole

Arvicola nivalis Martins, 1842:331. Type locality: "inside the Faulhorn Inn, at 2708 m above sea level", Bernese Oberland, Switzerland.

Synonyms. *Hypudaeus syriacus* Brants, 1827; *H[ypudaeus] alpinus* Wagner, 1843; *A[rvicola] lebrunii* Crespon, 1844; *Hyp[udaeus] nivicola* Schinz, 1845; *Arvicola leucurus* Gerbe, 1852; *Hypudaeus petrophilus* Wagner, 1853; *Microtus nivalis aquitanius* Miller, 1908; *Microtus ulpius* Miller, 1908; *Microtus pontius* Miller, 1908; *Microtus hermonis* Miller, 1908; *Chionomys appenninicus* [Forsyth] Major, 1909 [nomen nudum]; *M*[*icrotus*] *(Chion*[*omys*]*) nivalis trialeticus* Shidlovskiy, 1919; *Microtus (Chionomys) nivalis satunini* Shidlovskiy, 1919; *Microtus nivalis Malyi* Bolkay, 1925; *Microtus nivalis appenninicus* Dal Piaz, 1929; *Microtus (nivalis ?* [sic]*) mirhanreini* Schaefer, 1935; *Microtus (Chionomys) nivalis abulensis* Agacino, 1936; *Microtus (Chionomys) nivalis olympius* Neuhäuser, 1936; *Microtus (Chionomys) nivalis*

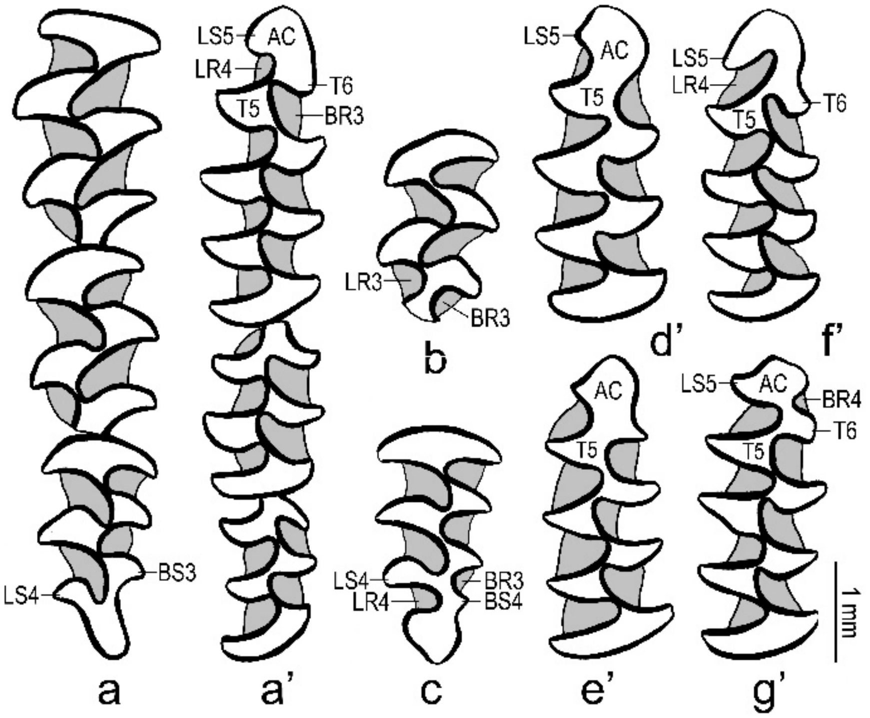


Figure 167: Grinding molar pattern in European snow vole. *Chionomys nivalis*: upper (a) and lower (a') row (Kopetdag, Turkmenistan); b–isolated M^2 (Güzyürdu, Turkey), c–isolated M^3 (Tatra Mts., Slovakia). Isolated M_1: d'–Cordillera Cantabrica, Spain; e'–Mt. Uludağ, Turkey; f'– Rodnei Mts., Romania; g'–Güzyürdu, Turkey.

dementievi Heptner, 1939; *Chionomys nivalis wagneri* V. Martino & E. Martino, 1940; *Microtus (Chionomys) radnensis* Éhik, 1942; *Microtus (Chionomys) nivalis loginovi* Ognev, 1950; *Chionomys nivalis aleco* Paspaleff, K. Martino & Peshev 1952; *Microtus (Chionomys) nivalis cedrorum* Spitzenberger, 1973; *Ch[ionomys] nivalis pirinensis* Kratochvíl, 1981; *Ch[ionomys] nivalis pirinensis* natio *rilensis* Kratochvíl, 1981 [nomen nudum]; *Ch[ionomys] nivalis balcanicus* Kratochvíl, 1981; *Ch[ionomys] nivalis balcanicus* natio *slavianka* Kratochvíl, 1981 [nomen nudum]; *Ch[ionomys] nivalis cantabricus* Kratochvíl, 1981; *Chionomys nivalis spitzenbergerae* Nadachowski, 1990; *Chionomys layi* Zykov, 2004.

Taxonomy and nomenclature. For the status of *layi* see Mahmoudi et al (2017c). Bannikova et al. (2013) reported a single highly divergent *Cytb* haplotype from the Central Taurus Mts. (Turkey) which they linked to *spitzenbergerae*. In the past topotypes of *spitzenbergerae* were misclassified as *C. gud* (Spitzenberger 1971) but Arslan et al. (2017) demonstrated that their *Mt*-DNA is indistinguishable from *C. nivalis*. The oldest well-supported lineage of *C. nivalis* was retrieved from the Kopetdag Mts. and Binalud Mts. at the eastern edge of the species range. *Cytb*-divergence is indicative of the intraspecific level and in captivity the Kopetdag voles freely hybridised with conspecifics from Europe (Yannich et al. 2012, Mahmoudi et al. 2017c).

Re-examination of the type for *Hypudaeus syriacus* Brants, 1827, showed that the voucher is identical to the European snow vole (Kryštufek et al. 2021), although since the 1970s it has consistently been listed in the synonymy of *Microtus socialis* (Musser & Carleton 2005). Referring to the principle of priority the valid name combination for the European snow vole is *Chionomys syriacus* (Brants, 1827) which predates *C. nivalis* (Martins, 1842) by 15 years. Since several authors writing after 1899 used *syriacus* as a valid name, it is not nomen oblitum (Article 23.9.1 of the Code). A strict adherence to the priority rule would destabilise the nomenclature, the case has been submitted to the International Commission on Zoological Nomenclature (ICZN) with a request to use its plenary power and protect *Arvicola nivalis* Martins.

Distribution (Figure 168). The range is scattered across the mountainous regions between north-eastern Portugal and Spain (Cordillera Cantabrica, Central System, Sierra de Segura, and Sierra Nevada) in the west, and Kopetdag (Turkmenistan), Binalud Mts. (north-eastern Iran) and Kerman (south-eastern Iran) in the east. The species is widespread in the Pyrenees, Massive Central, the Alps (France, Switzerland, Liechtenstein, Italy, Austria, Slovenia and southern Germany), and in the mountains of the western Balkans, namely the Dinaric Alps (Slovenia, Croatia, Bosnia and Herzegovina, and Montenegro) and the Shar-Pindus Mts. (western North Macedonia and western Greece as far south as Peloponnese; also likely present in Albania). Further east and north, isolated fragments of variable size are located in the Rhodope Mts. and the Stara Planina Mts. (Bulgaria and eastern Serbia), and the Carpathians (Romania, south-western Ukraine, Slovakia), including the isolated Fagaras Mts. in north-eastern Romania. In the Middle East, localities cluster in the Lesser Caucasus (Georgia, Azerbaijan, north-eastern Turkey), but become more scattered across the Greater Caucasus in northern Georgia and adjacent Russia (Adygeya, Karachayevo-Cherkesskaya Republic, Krasnodar, Severnaya Ossetia and Dagestan). Snow vole populations are similarly rare and dispersed in the Black Sea Mountains of northern Turkey (east of Mt. Uludağ), in the Taurus Mts. (east of Mt. Kohu Dağ), in Central (Mt. Ercyes Dağ) and Eastern Anatolia (east of the Euphrates), in Levant (western Syria, Lebanon, northern Israel), in north-eastern Iran (West and East Azerbaijan, and Ardabil), the Alborz Mts. and the Zagros Mts. The range is by far the largest of any snow vole, covering 598,835 km^2.

The European snow vole depends on fractured rocky substrate regardless of the elevation and was recorded in Europe at 30–5,070 m; the elevational range is narrower in the Middle East (700–3,500 m). The abundance of suitable habitats above the tree line and their scarcity at lower altitudes have resulted in the long-standing and widespread misbelief that the species is a high-altitude specialist requiring low summer temperatures (e.g. Miller 1912a). In reality, the European snow vole shows no special adaptations to the temperature extremes of high altitudes (Kryštufek & Kovačić 1989). In the Mediterranean mountains it is present along the entire elevational gradient providing there are open rocky places available, but becomes abundant and widespread only above the timber line (Kryštufek et al. 2011). The European snow vole is rarely sympatric with *C. gud* and *C. lasistanius* which show similar habitat requirements (Kryštufek & Vohralik 2005, Sizhazheva & Dzuev 2011).

Characteristics (Figure 165a,b). Small to moderately large snow vole with proportionally the shortest tail in the genus (TL/H&B=0.42–0.57). Dimensions: BWt=30–78 g, H&B=107–143 mm, TL=46–82 mm, HF=16.8–23.8 mm, EL=11.0–18.0 mm, CbL=25.1–30.5 mm, ZgW=14.7–16.9 mm, MxT=6.0–7.9 mm. Hairs on the tail do not entirely conceal the annulations; the terminal pencil is rather weak (length=1.5–4 mm). Mystacial vibrissae are long (29–48 mm). The pelage is dense, soft and long (8.5–14.5 mm); with longer sprinkling hairs measuring 11–18 mm. Colour varies among populations from light-grey with buffy suffusion (pale-buff or straw-grey) to smoke-grey with a dull-brown tint; the back is grizzled by dark hair tips. Belly is buffy-white to gloomy-white, irregularly clouded by slaty hair bases. Demarcation along the flanks is usually faint. Tail colouration varies from white throughout to brown above and light grey or whitish below; feet are whitish, occasionally pure white. Glans penis is 4.4–5.2 mm long and ~3.6 mm wide. Baculum is comparatively large; basal stalk is 2.93–3.55 mm long and 1.58–2.20 mm wide across the base; the median distal digit is of moderate length (0.81–1.25 mm) but the lateral digits are short (0.20–0.35 mm) or remain cartilaginous (Aksenova 1980, Kryštufek & Vohralik 2005). Skull is as described above; interorbital region is broad and flat without clear supraorbital ridges or sagittal crest. Postorbital tubercles of squamosal bone are feeble (Figure 169); *squama carina media* is either low or high, depending on the population. A bony bridge between the posterior palatine foramen and the lateral pit (*fossa lateralis*) is present at various frequencies depending on the population (Kryštufek 1990). Incisors and molars are comparatively smaller than in *Microtus*. M_1: T5 is confluent with the anterior cap (AC; Figure 167e') and occasionally a deep BR4 isolates T6 from AC (Figure 167g'). Karyotype (2n=54, NF_a=52) consists of acrocentric autosomes of gradually decreasing size; the X chromosome is large submetacentric and the Y is small acrocentric (Zima & Král 1984).

Variation and subspecies. Phylogeographic reconstructions retrieved three divergent lineages, one European and two Asiatic. The lineage from Kopetdag (southern Turkmenistan) and the Binalud Mts. (northeastern Iran), which holds the basal position in the *C. nivalis* tree, was classified as ssp. *dementievi* (Yannic et al. 2012). Asiatic lineages are in a sister position against the European samples; their sub-structuring shows strong geographic associations (Mahmoudi et al. 2017c). At some point in time they were classified into

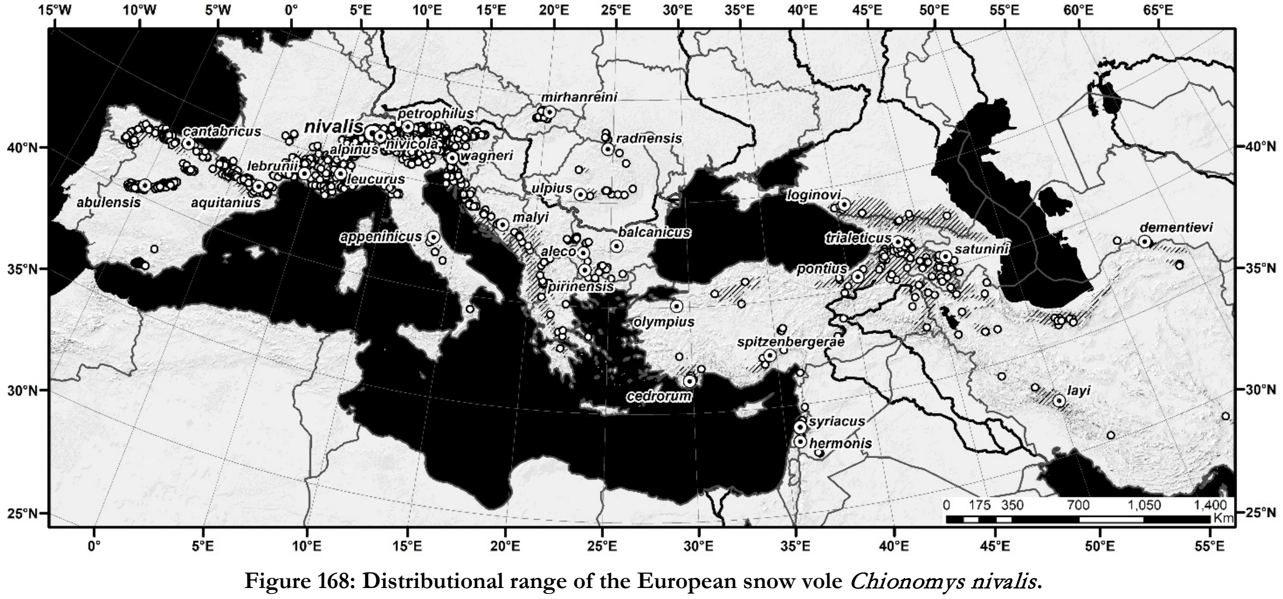


Figure 168: Distributional range of the European snow vole *Chionomys nivalis*.

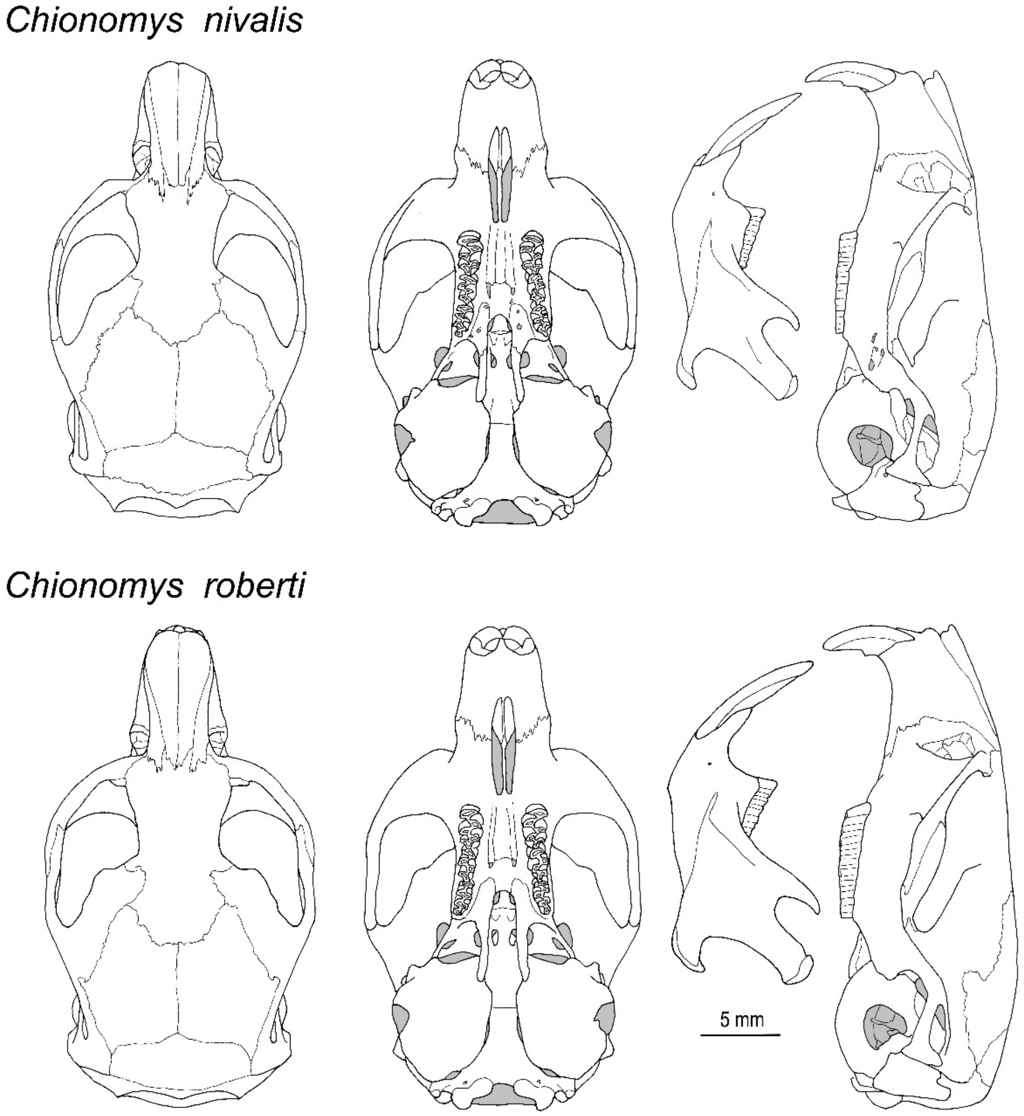


Figure 169: Skull in *Chionomys nivalis* (top; Qutur Su, Ardabil, Iran) and *C. roberti* (bottom; Trabzon, Maçka, Turkey).

nine nominal subspecies. The European lineage is substructured into two sub-lineages, the Southern (from Spain to the Eastern Carpathians and the Balkans) and the Northern (the Alps and Western Carpathians). These lineages broadly overlap in Peninsular Italy and the Western Alps, presumably due to secondary admixture. Up to 15 subspecies were recognised from Europe alone (e.g. Kratochvíl 1981).

Phenetic distances among European snow vole populations do not relate to the phylogenetic architecture and traditional subspecies are frequently at odds with morphologically diagnosable populations (Kryštufek et al. 2015b). Pelage colouration, skull and molar pattern vary independently and respond idiosyncratically to narrow local conditions. It has therefore been suggested that the subspecies is not an adequate category for describing the complex geographic variation in *C. nivalis* (Kryštufek 1990).

SUBGENUS: *Protochionomys* new subgenus

Taxonomy. The new subgenus has an identical taxonomic scope as the *roberti* species group of Ellerman (1941) and subsequent authors.

Type species. *Microtus roberti* Thomas, 1906.

Etymology. The name *Protochionomys* was coined from "protos" (πρῶτος) meaning "first" and *Chionomys* which

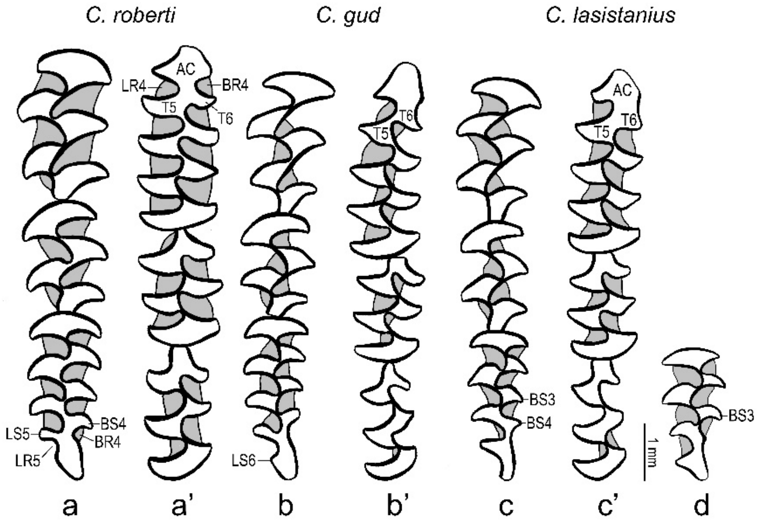


Figure 170: Grinding pattern of the upper (a–c) and lower molars (a'–c') in snow voles *Chionomys roberti* (a,a'–Çamlik, Turkey), *C. gud* (b,b'–Gudauri, Caucasus, Georgia), and *C. lasistanius* (c,c'–Ovitdağ Gecidi, Rize, Turkey; d–isolated M^3 from east of Ardahan, Turkey).

is of two parts, "chion" (χιών) meaning "snow" and the extension "mys" (μυς; all from Ancient Greek) for "mouse", therefore a "snow mouse". Protos is in allusion to the presumed cradle of the genus *Chionomys*, to which *Protochionomys* is entirely restricted.

Diagnosis and comparisons. Phylogenetic analysis of *Mt*-haplotypes and 3 Y-chromosome introns (*DBY7, DBY14, UTY11*; Yannic et al. 2012, Bannikova et al. 2013) retrieved *Protochionomys* as a monophyletic lineage holding a sister position against *C. nivalis* (subgenus *Chionomys*). The smallest autosomal pair is bi-armed (acrocentric in *Chionomys* s.str.); NF_a=54. Tail is comparatively long (TL/H&B>0.55), and the outer metatarsal pad is smaller (Figure 166a,b). The distal baculum is either completely ossified or the lateral digits remain cartilaginous. In comparison with *Chionomys* s. str., the skull is shallower and the bullae are smaller (bullae length/CbL=0.23–0.28). The base of M^{1-2} is without expansions or an additional postero-lingual salient angle. M^3 commonly has 4–5 lingual and 4 labial salient angles (Figure 170), hence the posteroconid complex is longer (>50% of M^3 length). M_1 shows confluent dental fields T5–T6 in >90% of cases.

Content. The new subgenus contains 3 extant species: *Chionomys roberti*, *C. gud* and *C. lasistanius*.

Distribution. The Caucasus and the Black Sea Mts. in Turkey as far west as the Yesilırmak River.

Species group *gud*

The *gud* species group contains two rock dwelling species, *gud* and *lasistanius*.

Chionomys gud (Satunin, 1909) – Gudaur Snow Vole

Microtus gud Satunin, 1909:272. Type locality: "Alm Tarpank from the Abusar-dagh, Kr. [District of] Olty (7000') [2,135 m]"; now "near Gudaur Pass" (Ognev 1950:435), Georgia.

Synonyms. *M*[*icrotus*] *(Chion*[*omys*]*) nivalis oseticus* Shidlovskiy, 1919; *M[icrotus*] *(Chion*[*omys*]*) nivalis oseticus,* ab[eratio] *lucidus* Shidlovskiy, 1919 [nomen nudum, valid from Ellerman 1941:606]; *M*[*icrotus*] *(Chion*[*omys*]*) nivalis lghesicus* Shidlovskiy, 1919; *M*[*icrotus*] *(Chion*[*omys*]*) nivalis lghesicus,* nat[io] *gotschobi* Shidlovskiy, 1919 [nomen nudum]; *Chionomys nivalis nenjukovi* Formozov, 1931.

Taxonomy. During the first half of the past century, *gud* was synonymised with *nivalis* and started to be treated as a species in its own right in the 1940s (Ellerman 1941, and subsequent authors).

Distribution (Figure 171). Endemic to the Greater Caucasus in northern Georgia, north-western

Azerbaijan, and Russia (Adygeya, Dagestan, Kabardino-Balkariya, Karachayevo-Cherkesiya, Krasnodarsk Krai, North Osetiya, and Stavropol' Krai). The area measures 81,075 km^2 and the elevational range is 410–4,190 m. This is a rock-dwelling vole, populating cracks in limestone and clay shale boulders, screes and caves. Typically lives in the (sub)alpine meadows above the timber line but also descends into the forest zone (Nasimovich 1935, Tembotov 1960).

Characteristics. Externally similar to *nivalis* but the tail is proportionally longer (TL/H&B=0.54–0.77). Dimensions: BWt=35–68 g, H&B=113–152 mm, TL=58–106 mm, HF=18.0–24.0 mm, EL=15–18 mm, CbL=25.0–31.6 mm, ZgW=14.1–18.4 mm, MxT=6.0–8.3 mm. Pelage is 7–9 mm long with protruding hairs measuring 12.5–13 mm; vibrissae are of similar length as in *nivalis*. The tail is sparsely hairy with an exposed annulation; the terminal pencil is feeble (length≈2 mm). The lateral metatarsal pad is small (as in *roberti*; Figure 166b). Glans penis is on average 4.8 mm long and 2.7 mm wide. Baculum has a well-ossified distal trident; length of medial and lateral digits is 1.50–1.60 mm and 0.92–1.05 mm, respectively. The proximal stalk measures 3.05–3.20 mm in length and 1.80–1.90 mm in width; the base has a distinct notch (Aksenova 1980). The skull is of similar size and proportion as in *nivalis* (ZgW/CbL=0.53–0.58) with the exception of being shallower and having shorter bullae. Temporal ridges are weakly expressed but the postorbital knob on the squamosum is usually powerful; the mandible is slender (Figure 172). Molar pattern: M^3 usually has four inner and outer salient angles; ~14% of individuals have an additional postero-lingual salient angle (LS6; Figure 170b). M_1 is like in *nivalis* but T5 and T6 have confluent dental fields in the vast majority of cases; these fields are isolated in ~5% of cases (Nadachowski 1991; see Figure 170b'). Karyotype is as in the subgenus; Y chromosome is of variable size (Sablina et al. 1988, Kryštufek & Vohralik 2005).

Variation and subspecies. Three loosely defined subspecies are usually recognised: *gud* (pelage light-grey to mouse-grey; size medium), *nenjukovi* (pelage grey to dull-brown, occasionally with an indistinct drab tint; size large), and *lghesicus* (resembles the nominal subspecies but is smaller) (Ognev 1950, Gromov et al. 1963). Phylogeographic analysis retrieved four divergent lineages; voles in two lineages were classified as sspp. *gud* and *nenjukovi*, respectively, one lineage contained two

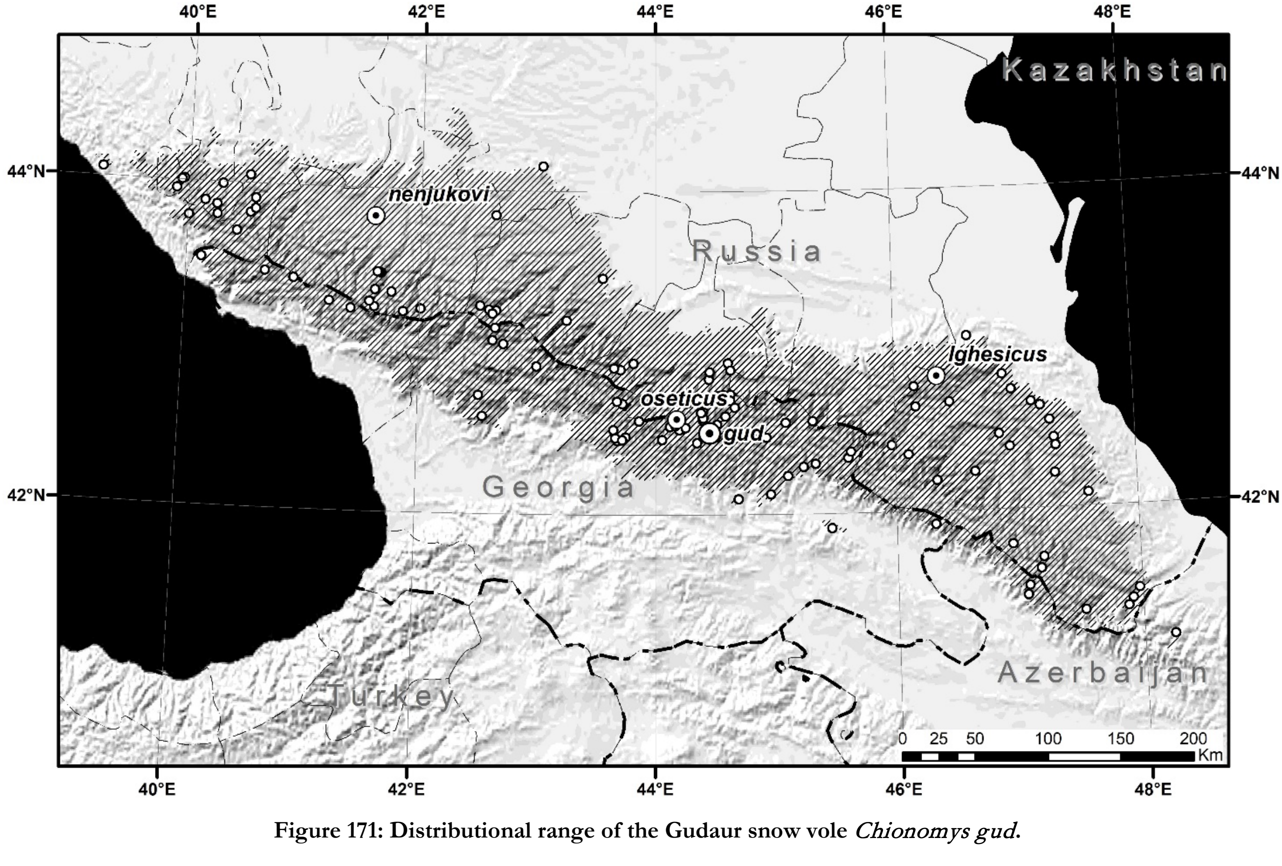


Figure 171: Distributional range of the Gudaur snow vole *Chionomys gud*.

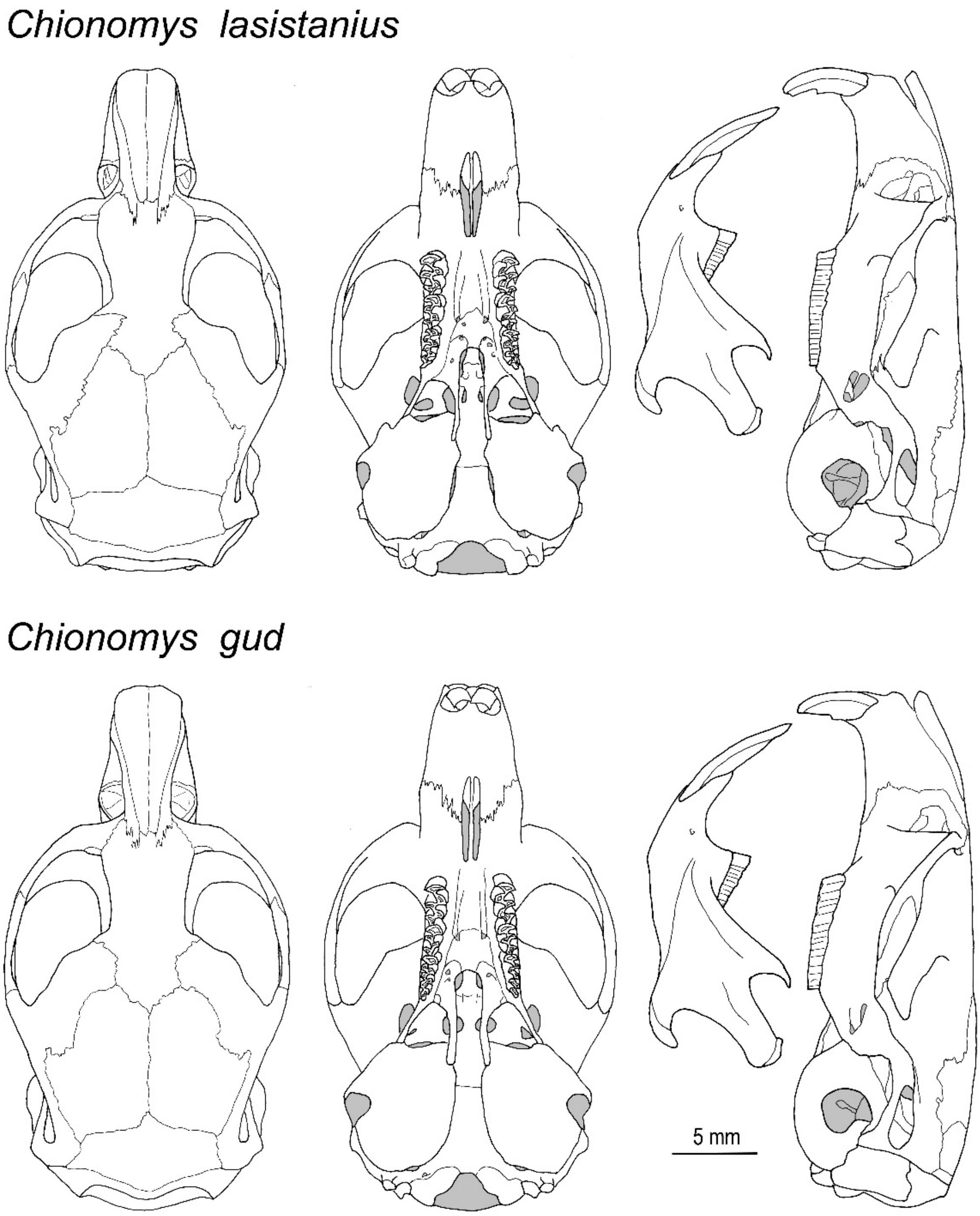


Figure 172: Skull in *Chionomys gud* (top; Gudauri, Greater Caucasus, Georgia) and *C. lasistanius* (bottom; Ovit İkizdere, Rize, Turkey).

subspecies (*gud* and *lghesicus*), and one lineage is still unnamed (Bannikova et al. 2013).

Chionomys lasistanius (Neuhäuser, 1936) – Lazistan Snow Vole

Microtus (Chionomys) gud lasistanius Neuhäuser, 1936a:160. Type locality: "Versambeg-Dag [Dağ=Mountain], Vilayet [Province of] Rize", Turkey. The type locality is possibly identical to Vercenik Dağ, west of Elevit (Kryštufek & Vohralík 2005:225).

Taxonomy. Described as a subspecies of *C. gud* and elevated to a species in its own right (Pardiñas et al. 2017) on the basis of genetic metrics (Bannikova et al. 2013).

Distribution (Figure 173). Occupies an area of 13,425 km² in the Lesser Caucasus of southern Georgia and extreme north-eastern Turkey (Artvin, Giresun, Kars, Rize). Elevational range is 1,440–3,300 m. Lives in rocky habitats like other rock-dwelling snow voles but prefers more humid situations than *nivalis*. Present inside the forest belt and in alpine pastures. Rarely syntopic with *nivalis* (Kryštufek & Vohralik 2005); presumably

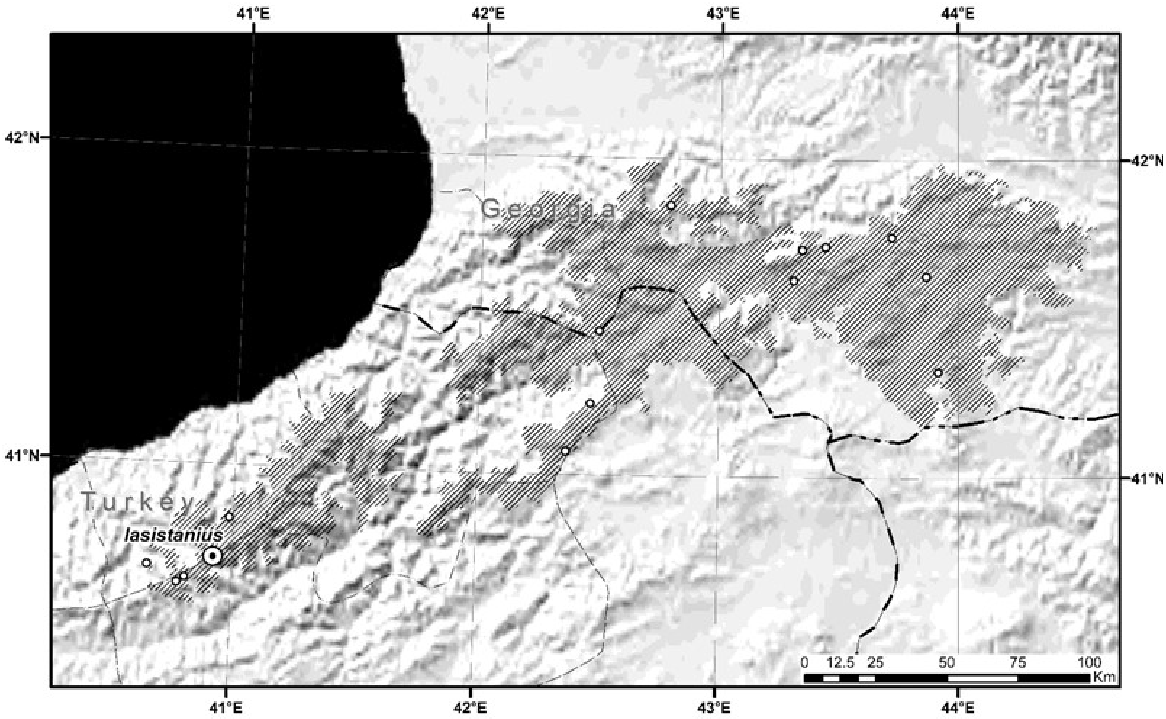


Figure 173. Distributional range of the Lazistan snow vole *Chionomys lasistanius*.

outcompeted from the forest belt by *roberti* (Steiner 1972).

Characteristics (Figure 165c). Externally and cranially closely resembles *gud*. Tail is proportionally longer (TL/H&B=0.54–0.67) than in sympatric *nivalis*; hairs do not conceal the annulation and the terminal pencil is feeble (length=2.5–5 mm). Vibrissae are long (35–42.5 mm). Dimensions: BWt=34–63 g, H&B=112–130 mm, TL=57–79 mm, HF=19.0–21.2 mm, EL=15.1–19.0 mm, CbL=27.3–30.1 mm, ZgW=15.4–17.4 mm, MxT=6.7–7.8 mm (Kryštufek 1999). Pelage is soft, dense and long (8.5–12 mm); sparse hairs are longer 1.5–4 mm. Dorsal fur is smoke-grey with a light brown shade while flanks have a more distinct drab tint. The belly is always grey and only slightly washed buff; there is no clear demarcation on the flanks. The tail is usually bi-coloured, blackish-brown above and grey below but the contrast fades in some animals. Feet are whitish to light-grey and ears are grey. Glans penis is 5.2 mm long and 2.9 mm wide (Sözen et al. 2009). The baculum is similar to *gud*, except that the medial distal digit is shorter (1.24–1.35 mm) and the base of the proximal bone lacks a notch. Dimensions are: length of stalk=2.76–3.21 mm, basal width=1.69–1.92 mm, length of lateral digit=0.96–1.13 mm (Kryštufek & Vohralik 2005). Skull closely resembles that of *C. gud*; braincase is shallow, temporal ridges are well-developed for *Chionomys* standards and merge to the inter-orbital crest in old individuals. The mandible is slender (Figure 172). Molars are as in *C. gud*; M^3 usually has 4 outer and inner salient angles; some voles show 3 salient angles on either or both sides (Figure 170d). Morphotypes of M_1 overlap with *gud* and *nivalis*; T5 is either isolated or confluent with T6 and AC. In rare instances T6 is isolated from AC. Conventionally stained karyotype is as in *C. gud*; the X chromosome is large submetacentric and the Y is small acrocentric (Sözen et al. 2009).

Variation and subspecies. Monotypic.

Species group *roberti*

The *roberti* species group contains a single species which is unique among Palaearctic voles for its semi-arboreal lifestyle.

Chionomys roberti (Thomas, 1906) – Robert's Snow Vole

Microtus Roberti Thomas, 1906b:418. Type locality is "Sumela [now Meryamana], […] south of Trebizond [Trabzon]", Turkey.

Synonyms. *Microtus (Chionomys) pshavus* Shidlovskiy, 1919; *Chìonomys personatus* Ognev, 1924; *Microtus roberti occidentalis* Turov, 1928; *Microtus roberti circassicus* Heptner, 1948 [substitute name for *occidentalis* Turov]; *Microtus roberti turovi* Hoffmeister, 1949 [substitute name for *occidentalis* Turov].

Taxonomy. A very distinctive member of *Chionomys*, externally readily recognisable by its larger size, dull brown pelage, and comparatively long tail; cranially differs from *gud-lasistanius* by proportionally smaller bullae. Due to these peculiarities, in addition to a complex molar pattern, Miller (1908a) did not include *roberti* into his newly established *Chionomys*. Similarly, Neuhäuser (1936b) incorporated *nivalis* and *gud* in *Chionomys*, but considered *roberti* to belong to the "true" *Microtus*.

Distribution (Figure 174). Present throughout the Caucasus and the north-eastern Black Sea Mts., as far west as the Yesilırmak River. Its range of 81,375 km² centres in north-eastern Turkey (Artvin, Giresun, Trabzon, Rize, Ordu) and Georgia (Abkhazia, Ajaria, Guria, Imeret'i, Kakhet'i, K'vemo K'art'li, Mts'khet'a-Mt'ianeti, Racha-Lech'khumi and K'vemo Svanet'i, Samegrelo-Zemo Svanet'i, Samts'khe-Javakhet'i, and Shida K'art'li). From Georgia, the range extends into north-western Azerbaijan (Balkan, Qakh) and Russia (Adygeya, Dagestan, Karachayevo-Cherkesiya, Krasnodar, and North Ossetia). Elevational range is 165–2,550 m with a single record in Dagestan from 3,000 m. Preferred habitat is dense understory in humid forests, frequently along rivulets and streams on mountain slopes. Robert's snow voles avoid steep rocky banks, flooded lowlands and xerophilous woodland; in the subalpine belt they live inside dwarf shrub vegetation (Tembotov 1972). Earlier authors (e.g. Gromov et al. 1963) stipulated a semi-aquatic lifestyle for *C. roberti*, similar to *Arvicola*. This vole, however, is semi-arboreal (Pecheniuk 1974).

Characteristics (Figure 165d). The largest snow vole with the longest tail (TL/H&B=0.57–0.81). Dimensions: BWt=40–78 g, H&B=125–156 mm, TL=80–108 mm, HF=21.7–24.9 mm, EL=14–20 mm, CbL=28.8–32.9 mm, ZgW=15.5–18.5 mm, MxT=6.7–8.6 mm. Fur is of medium texture; hairs are 9.5–12 mm long and protruding hairs are longer by 3–5 mm. The appearance is less chunky than in *C. nivalis*; vibrissae measure 35–45 mm. The metacarpal pads are smaller than in the remaining snow voles (Figure 166a'). Hairs on the tail are scarce and the annulation is fully exposed;

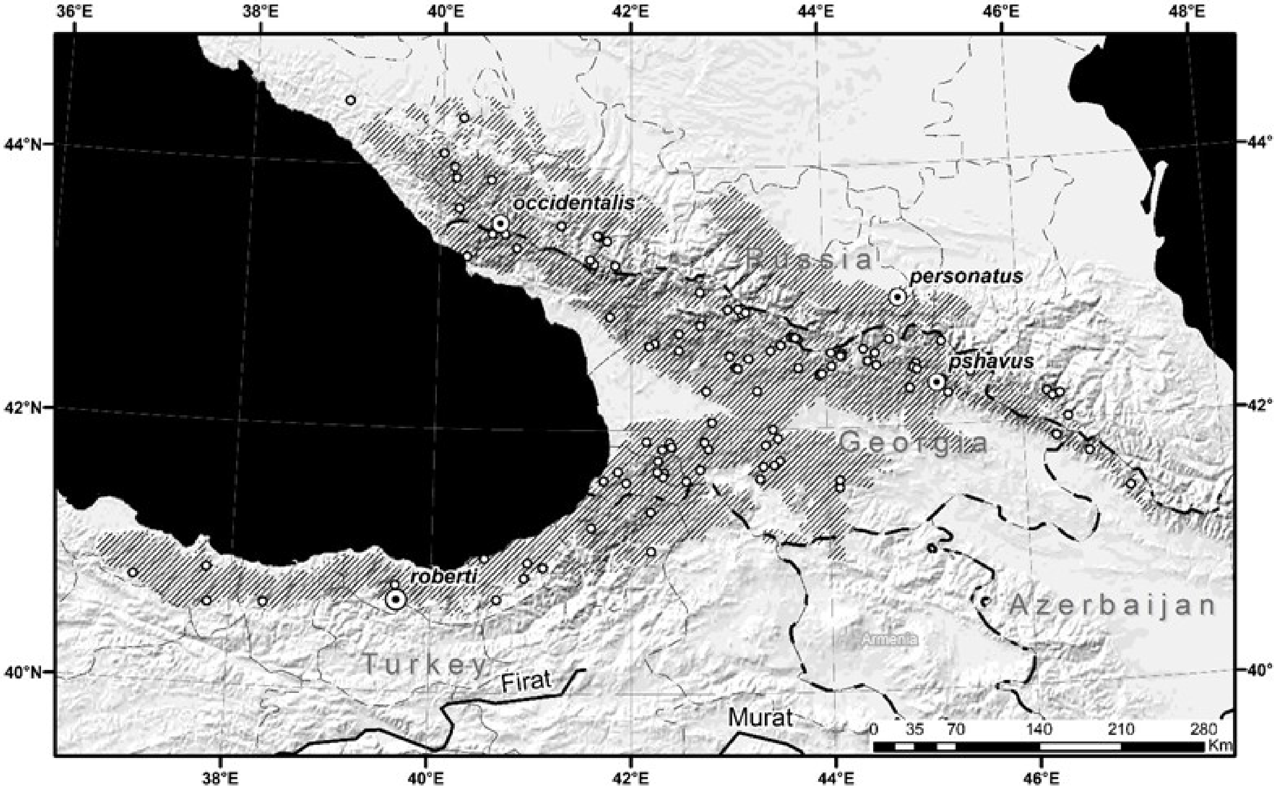


Figure 174: Distributional range of Robert's snow vole *Chionomys roberti*.

the terminal pencil is scant (length=2.5–4.5 mm). The back is brown (nearest to mummy-brown) and the belly is smoke grey with a slight drabby suffusion. Demarcation along flanks is fairly distinct. The tail is indistinctly bi-coloured, blackish above and grey below. Greyish feet are occasionally washed buffy; ears are grey. Juveniles are darker with a slate belly, grey feet and a nearly uniformly dark tail. Shape of baculum is more variable than in other snow voles. The proximal baculum is 2.87–3.77 mm long and 1.58–2.08 mm wide across the base. The medial distal digit is of variable length (0.90–1.30 mm) and is always weaker than in the *gud* species group. The lateral digits may remain cartilaginous; when ossified, they vary from tiny circular to rod-like elements up to 0.75 mm long (Kryštufek & Vohralik 2005).

Skull is of similar proportions as in *gud* (ZgW/CbL=0.55–0.58); ridges are weak and the postorbital tubercles of *squamosum* are less prominent than in *C. gud-lasistanius*; bullae are short (length of bullae/CbL=0.23-0.29). Mandible is more robust than in other snow voles (Figure 169). All molar morphotypes reported for *gud* occur in *roberti* (Figure 170a), although there is a slight difference in proportions; M^3 has a significantly higher incidence of five inner salient angles (66% in *roberti v.* 14% in *gud*; Nadachowski 1991). Conventionally stained karyotype is as in *gud* (Sablina et al. 1988).

Variation and subspecies. Either regarded as monotypic (Ognev 1950, Gromov et al. 1963, Gromov & Erbajeva 1995) or split into five subspecies (Gromov & Polyakov 1977). Various datasets indicate geographic variation but the phenomenon was never comprehensively assessed or translated into a subspecific taxonomy. The Y chromosome is small in the Caucasus (Sablina et al. 1988) and large in Turkey (Kefelioğlu 1995). The anterior cap and T7 of M_1 are isolated from T5–T6 in 12.5% of topotypes of *roberti*, while they are invariably confluent in the Western Caucasus (topotypes of *occidentalis*; Nadachowski 1991). Phylogeographic screening retrieved geographically meaningful *Mt*-lineages but denser sampling is required for firm conclusions (Bannikova et al. 2013).

GENUS: *Proedromys* Thomas, 1911 – Groove-toothed Voles

Proedromys Thomas, 1911a:4. Type species by monotypy is *Proedromys bedfordi* Thomas.

Taxonomy. Three genera (*Proedromys, Mictomicrotus* new genus, and *Volemys*) from the mountains of Sichuan, adjacent to Xizang and Gansu are phylogenetically isolated within Microtina, showing singular mosaics of acquired and ancestral traits. Little is known about these genera. Throughout the entire 20th century, *Proedromys bedfordi* was known only from the type while a mere six vouchers of *Volemys millicens* were available. On the other hand, *Volemys musseri* and *Mictomicrotus liangshanensis* were named as late as 1982 and 2007, respectively. Karyotype has not yet been studied in these voles.

Proedromys was described as a genus in its own right although some authors (Simpson 1945, Ellerman & Morrison-Scott 1951) relegated it to a subgenus of *Microtus*. Molecular phylogenetic reconstructions retrieved affinities with *Lasiopodomys* and *Stenocranius* (Fabre et al. 2012) or with a cluster containing these two genera in addition to *Alexandromys* and *Neodon* (Chen et al. 2012). Steppen and Schenk (2018) stipulated sister relationships between *Proedromys* and *Volemys* and their basal position in Microtina (after the exclusion of *Chionomys*). Other authors saw *Proedromys* as a close relative to the fossil *Allophaiomys* or to some ancestral *Lasiopodomys* (Repenning 1992b), to *Neodon* (Martin 1969) or to *Lasiopodomys* and *Blanfordimys* combined (Robovský et al. 2008). The fossil record of *Proedromys* is >1Mya old (Repenning 1992b). The genus contains two species (Pardiñas et al. 2017), but we exclude *liangshanensis* from its scope.

Proedromys bedfordi Thomas, 1911 – Groove-toothed Vole

Proedromys bedfordi Thomas, 1911a:4. Type locality: "60 miles [97 km] S.E. [south-east] of Min-Chow [Minchow], Kan-su [Gansu]. 8000' [2,440 m]" (Thomas 1911.e:177), China.

Distribution (Figure 175). Known from 3 localities in the Hengduan Mts. in northern Sichuan (near Heishui and Jiuzhaigou) and 1 locality in southern Gansu. The entire range covers 5,020 km^2 of grassland at medium elevations (1,830–2,770 m). Fossil range was likely more extensive and also encompassed the provinces of Shanxi, Hubei, and Shandong (Zheng & Li 1990).

Characteristics. A medium sized vole, externally resembling *Microtus*. Dimensions: BWt=40–42 g, H&B=100–129 mm, TL=36–44 mm, HF=17–20.58 mm, EL=11–18 mm, CbL=24.1–27.0 mm, ZgW=14.1–16.2 mm, MxT=5.7–6.8 mm. The tail is moderately long (TL/H&B=0.32–0.41) and densely haired; the ears overtop the fur. Pelage is long (~16 mm), soft and dense; dorsal side is dull brown, the flanks are brighter and the belly is slaty with a brownish tint; the colours of the dorsum and the belly shade into each other without a clear demarcation on the flanks. The tail is bi-coloured, having a narrow brown stripe above and whitish underside; paws are dull-white and the light brown ears are hairy. There are 6 plantar pads and females have 8 nipples. Glans penis is short (length=3.2–3.5 mm) and wide (=2.3–2.4 mm); baculum is of trident type but the lateral digits remain cartilaginous. The medial distal baculum (length=0.75–0.83 mm) is ~⅓ the length of the proximal baculum, which is 2.67–3.82 mm long and 1.33–1.50 mm wide; lateral digits are cartilaginous (Liu et al. 2007).

Skull is heavily built and deep (height behind M^3≈37% of skull length); the dorsal profile is evenly bowed. The braincase is long (>½ the skull length) and moderately wide (ZgW/CbL=0.57–0.60). Temporal ridges extend from the lacrimal bone to the fronto-parietal suture; the post-orbital processes of the squamosal are prominent and peg-like. The nasals are rather short and do not hide the incisors from above; the interparietal is large. Incisive foramina are long; the median septum on the posterior palate is moderately wide and the lateral pits are deep. The auditory bullae are of normal size and contain spongy tissue. The mandible is robust with a

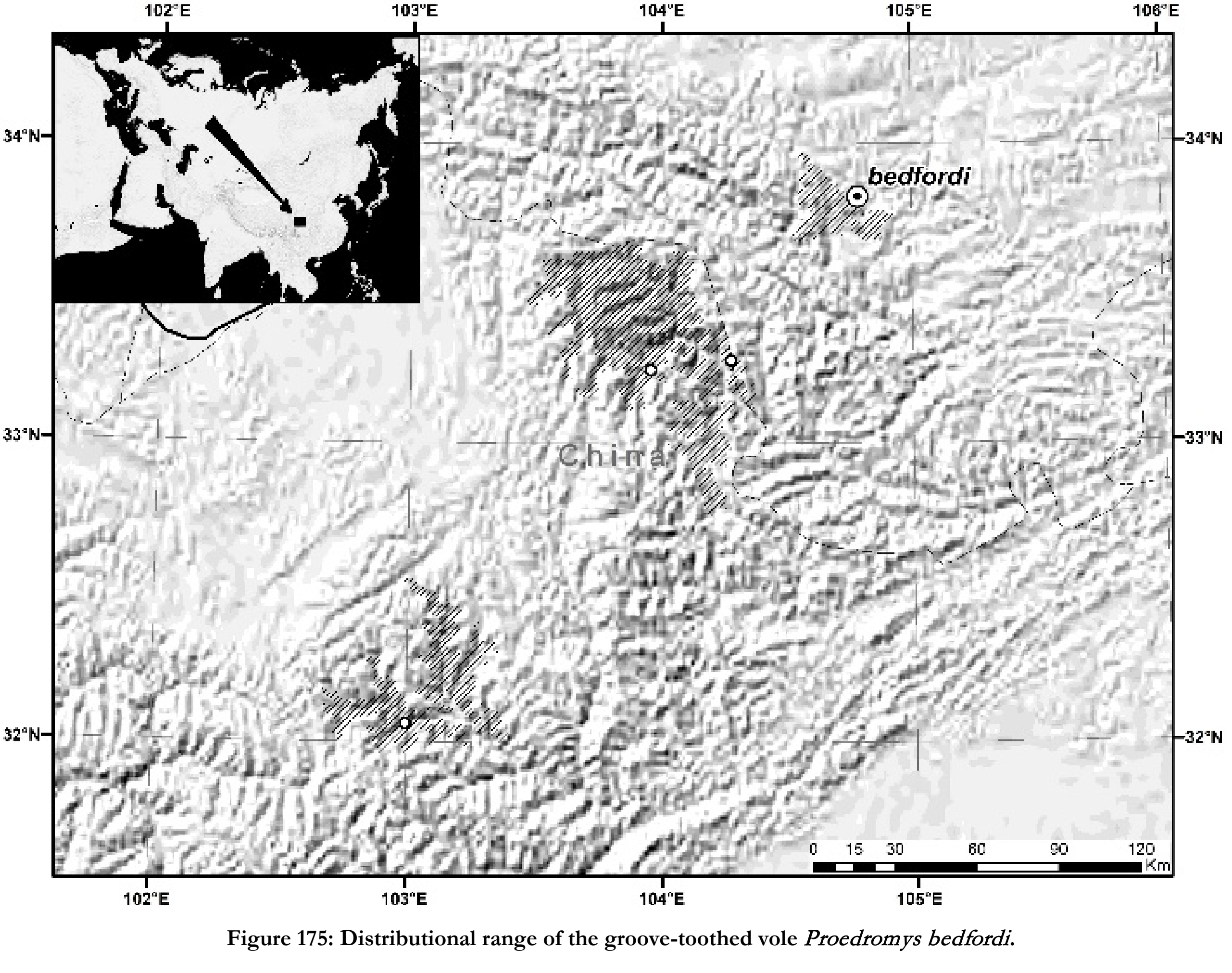


Figure 175: Distributional range of the groove-toothed vole *Proedromys bedfordi*.

deep body and prominent dorsal and ventral masseter crests on the outer surface; of the three processes, the coronoid is blunt, the articular is of normal size and the angular is comparatively long and slender (Figure 176). Dentition is highly distinctive. Upper incisors are broad ($\bar{x}$=2.62 mm; Liu et al. 2007) with a deep groove on the anterior surface shifted towards the lateral edge. Lower incisors are short, scarcely invading the condylar process. Molars have re-entrant angles abundantly filled with cement; the enamel is progressively differentiated and dental spaces are rather large. M^1–M^2 are like in *Microtus*; M^3 is shorter than M^2 and consists of only 2 alternating triangles between the anterior loop and the posterior cap, hence it has a single inner and two outer re-entrant angles. The anteroconid complex is rudimentary, consisting of alternating triangles (T4–T5) and a simple anterior cap which is confluent with T5; the other salient angles are markedly smaller than the inner ones. M_2 is as in *Microtus*; M_3 effectively consists of transverse loops with rudimentary outer salient angles T2 and T4 (Figure 177a).

Variation and subspecies. Monotypic species.

GENUS: *Mictomicrotus*, new genus – Liangshan Voles

Taxonomy. Contains a single species (*liangshanensis*) which was originally described as a member of *Proedromys* (Liu et al. 2007). *Proedromys bedfordi* and *liangshanensis* are not sister taxa in phylogenetic trees (Chen et al. 2012, Steppan & Schenk 2017) and profoundly differ morphologically (Liu et al. 2007). We hereby establish a new genus for the Liangshan vole, which is possibly a sister taxon to a clade of *Lasiopodomys, Stenocranius, Neodon, Alexandromys*, and *Microtus* (Chen et al. 2012, Steppan & Schenk 2017).

Type species: *Proedromys liangshanensis* Liu, Sun, Zeng & Zhao, 2007.

Etimology. The prefix "mictos-" (μικτός) means "mixed" in Ancient Greek; *Microtus* is a generic name for the central genus of Microtina and is composed of "mikros" (μικρός; meaning small) and "otos" (ὠτός for ear; both Ancient Greek), alluding to the short ears of these voles. The resulting name *Mictomicrotus* (a mixed *Microtus*) makes reference to the mixture of archaic and advanced characteristics in the genus.

Diagnosis and comparisons. *Mictomicrotus* differs from all other Microtina (including *Proedromys*) in *GHR* and *IRBP –RBP3* sequences (Chen et al. 2012). Morphologically, it is unique in the subtribe Microtina in combination with the following traits: (i) broad upper incisors with a smooth anterior surface; (ii) short lower incisors which barely reach the articular process (similar to *Proedromys*); (iii) M^3 with only two re-entrant angles on either side and a short, simple heel (similar to *Lasiopodomys, Blanfordimiys* and some *Terricola*); (iv) distal baculum is nearly as wide as it is long (Liu et al. 2007).

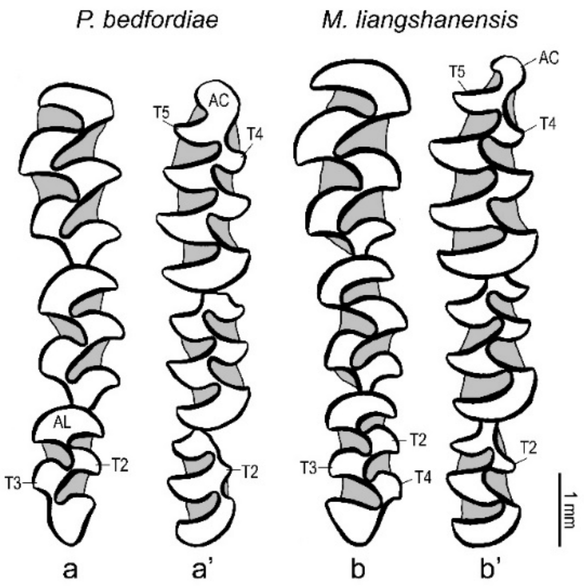
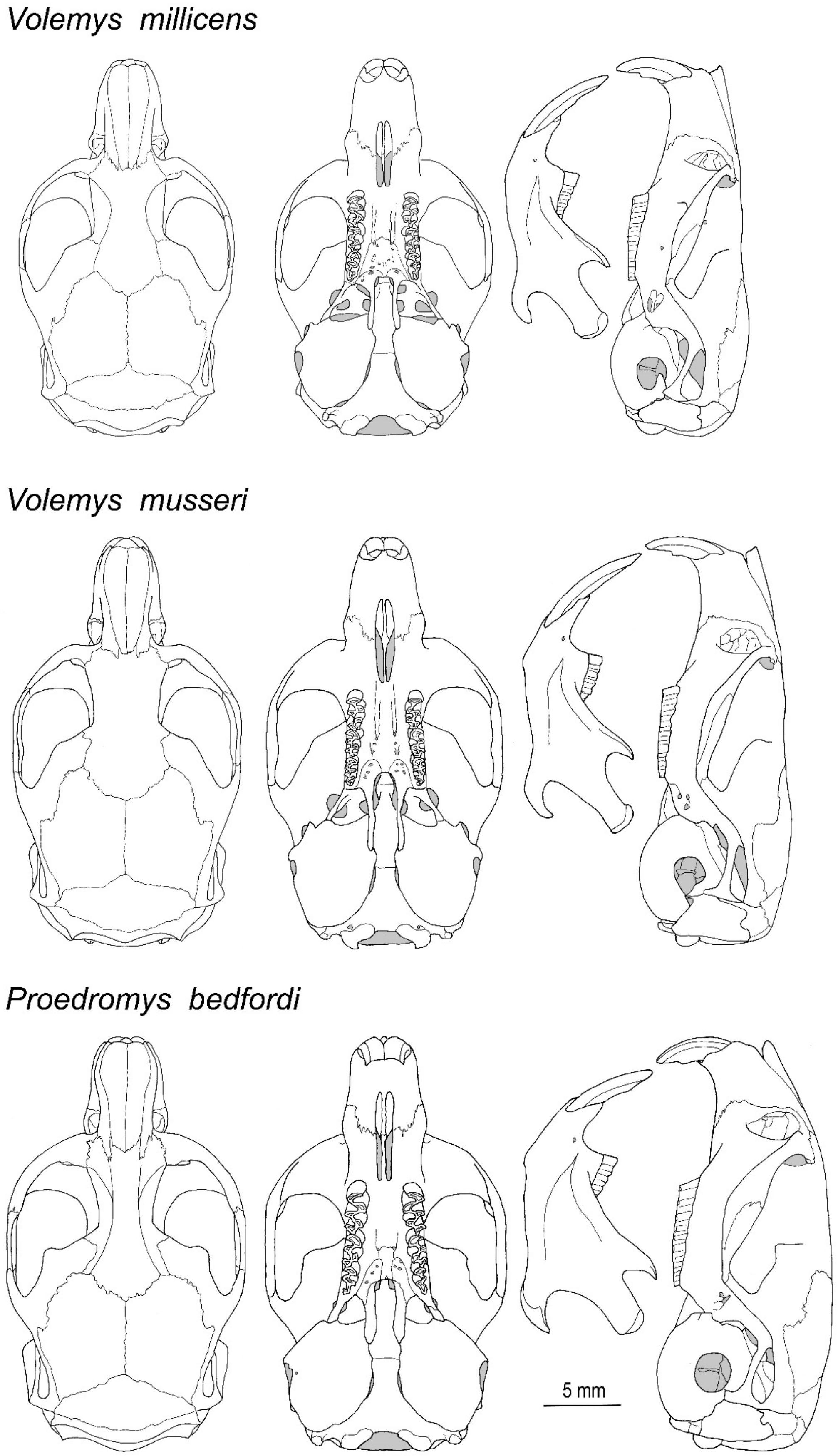


Figure 177: Upper (a,b) and lower (a',b') molars in *Proedromys bedfordi* (a,a'; Minchow, Gansu, China) and *Mictomicrotus liangshanensis* (b,b'; Mabian County, Sichuan, China).

Mictomicrotus liangshanensis (Liu, Sun, Zeng & Zhao, 2007) – Liangshan Vole

Proedromys liangshanensis Liu, Sun, Zeng & Zhao, 2007:1172. Type locality: "Mabian Dafengding National Nature Reserve, Mabian County", Sichuan, China.

Distribution (Figure 178). Known from Meigu, Mabian, and Jinyang counties in southern Sichuan, China, where it occupies fir and spruce forest at elevations of 2,560–3,100 m (Liu et al. 2007). The range covers an estimated 2,680 km².



Volemys millicens

Volemys musseri

Proedromys bedfordi

Figure 176: Skull in *Volemys millicens* (top; Weichow, western Sichuan, China), *V. musseri* (middle; 45km west of Wenquan, Sichuan, China), and *Proedromys bedfordi* (bottom; Minchow, Gansu, China).

Characteristics. Moderately large and long-tailed (TL/H&B>0.60) vole. Dimensions: BWt≈60 g, H&B=102–131 mm, TL=61–82 mm, HF=20–24 mm, EL=13–19 mm, CbL=28.9–31.5 mm, ZgW=15.3–17.3 mm, MxT=6.9–7.5 mm (Liu et al. 2007). Pelage is long and soft; the ears stick out slightly from the fur. There are 5 palmar and 6 plantar pads; females have 8 mammae. Dorsal pelage is yellow-brown; the belly is lighter and shaded yellow; the hair bases are slate. Transition on the flanks is gradual. Ears are grey and paws are whitish, both shaded yellowish. Glans penis is cylindrical with ventral furrow in its anterior half; it is 5.00–5.25 mm long and 3.20–3.75 mm wide. The proximal baculum (length=3.0–3.6 mm, basal width=1.8–2.1 mm) is heavy (width at mid-point=0.6–0.8 mm); lateral digits are of moderate size (length=0.92–1.0 mm; Liu et al. 2007). Skull is heavily built and the dorsal profile is flat with abruptly sloping nasals; zygomatic arches are expanded only slightly (ZgW/CbL≈0.53). The nasals are bottle-shaped; orbital region is like in *Microtus* s.str., with prominent temporal ridges. Incisors are orthodont; the upper ones are as wide as in *Proedromys* (=2.75 mm) but their outer surface is smooth. Molars are similar to *Proedromys* except that the size difference between the inner and outer triangles is more prominent. The anteroconid complex and the anterior cap (on M_1) are smaller; M^3 has three salient angles on either side and a broad but short posterior cap (Figure 177b).

Variation and subspecies. Monotypic.

GENUS: *Volemys* Zagorodnjuk, 1990 – Sichuan Voles

Volemys Zagorodnjuk, 1990 (in Zagorodnyuk 1990:28). Type species is *Microtus musseri* Lawrence.

Taxonomy. *Volemys* was established for 4 small-range voles occupying China (including Taiwan): *millicens, clarkei* (now in *Neodon), kikuchii (Alexandromys*) and *musseri*. Subsequent molecular analyses restricted the genus to *musseri* and *millicens* (Liu et al. 2017). Various taxa were proposed as close relatives to *Volemys*: *Chionomys* (Lawrence 1982), *Alexandromys* (Fabre et al. 2012), *Neodon* (Liu et al. 2017), and *Proedromys bedfordi*

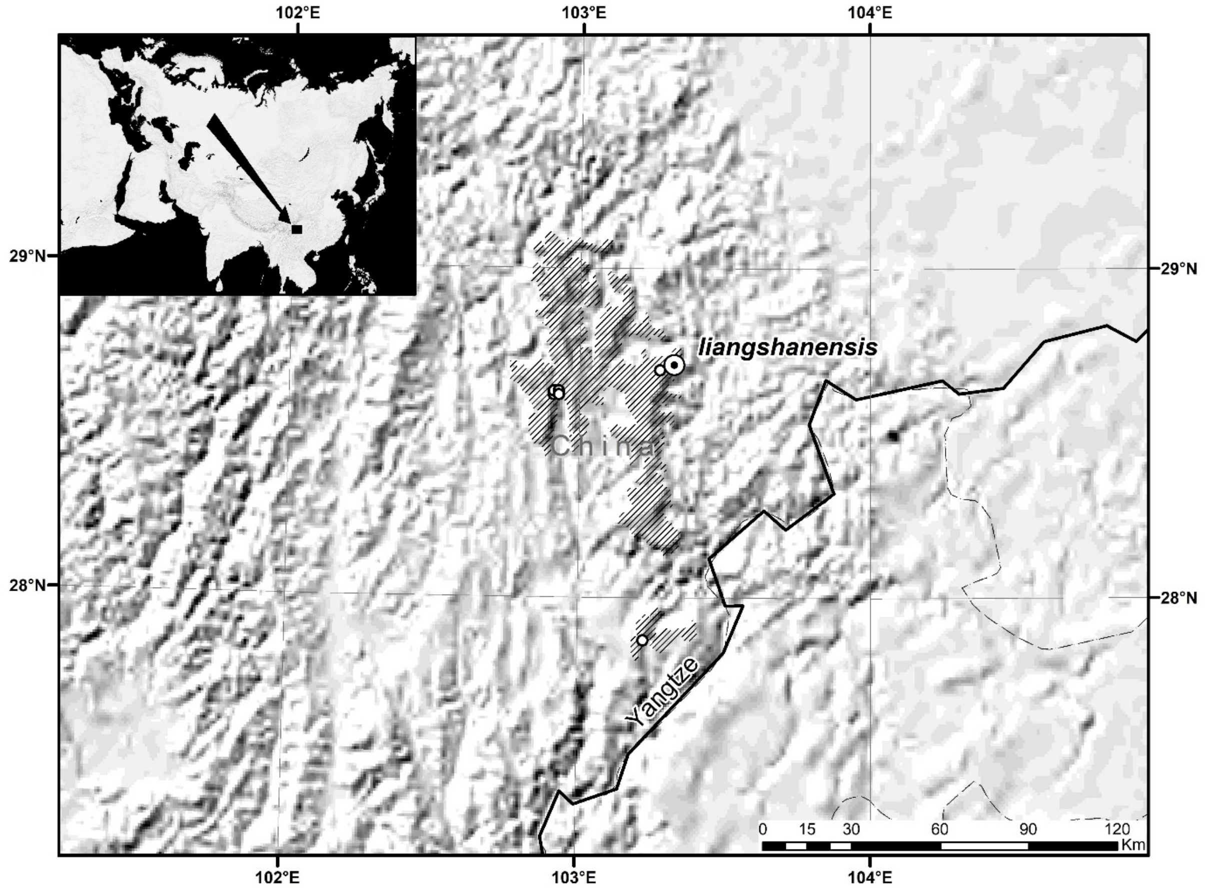


Figure 178: Distributional range of the Liangshan vole *Mictomicrotus liangshanensis*.

(Steppan & Schenk 2017). Pavlinov et al. (1995) classified *Volemys* as a subgenus of *Microtus*.

Distribution. High-altitudes of the eastern slopes of the Quinghai-Tibet plateau in Sichuan and adjacent Xizang (southern China). The two species are allopatric.

Characteristics. Moderately large and long-tailed voles; fur is long (~12 mm) and dark Females have 8 nipples and there are 6 plantar pads (Figure 179). The skull is lightly built and shallow with a long braincase and broad orbital region; temporal ridges are absent. The postorbital protuberances of the squamosal are weak and the interparietal is large. Mandible is low with a long, slender angular process (Figure 176). M^2 has an additional posterolabial salient angle (T5) which is never isolated. M^3 has 3 outer and 3–4 inner salient angles; M_1: T5 is confluent with the anterior cap which in turn communicates with salient angles LS5 and BS4. M_2: the anterior pair of triangles T3–T4 is confluent; T1–T2 alternate (Figure 180). Baculum is of trident type.

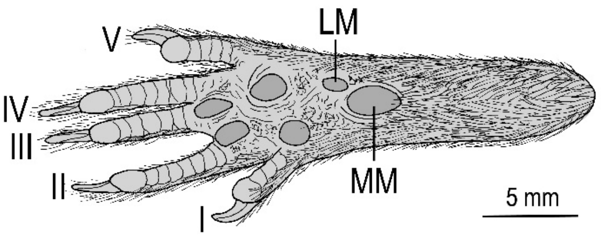


Figure 179: Left sole in *Volemys millicens* from Weichow, western Sichuan, China.

Key to species

1a) Tail proportionally shorter (TL/H&B<0.60); length of proximal baculum <4.7 mm; articular process is robust (width >½ height of mandibular corpus); M^1 with 3 lingual salient angles (T5 is absent) .... *millicens*
1b) Tail proportionally longer (TL/H&B>0.58); length of proximal baculum >4.7 mm; articular process is slender (width <½ height of mandibular corpus); M^1 with 4 lingual salient angles (T5 is present) .... *musseri*

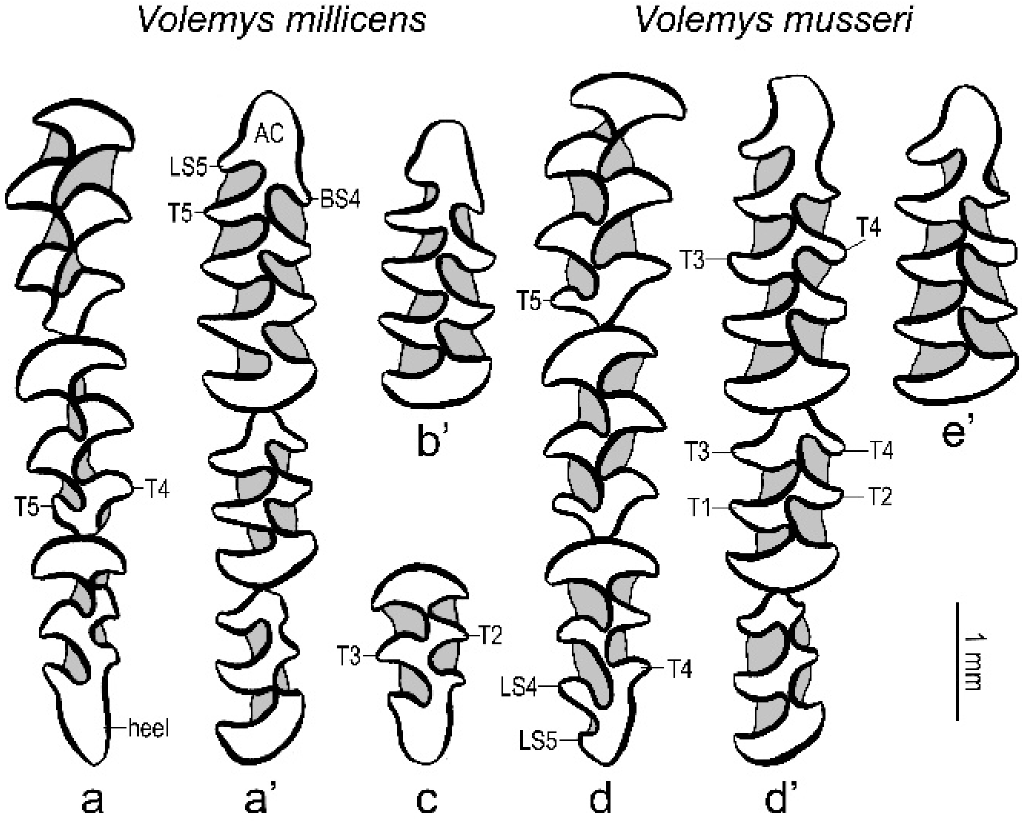


Figure 180: Molar pattern in Sichuan voles. *Volemys millicens*: upper (a) and lower row (a') and isolated M^3 (b) and M_1 (b'; all from Weichow, western Sichuan, China). *V. musseri*: upper (c) and lower row (c') and isolated M_1 (d'; all from 45km west of Wenquan, Sichuan, China).

Volemys millicens (Thomas, 1911) – Common Sichuan Vole

Microtus millicens Thomas, 1911b:49. Type locality: Weichow, "sixty miles [97 km] northwest of Chengtu [Chengdu] in the Si Ho or Sungpan Ho valley, northwestern Szechwan [Sichuan], China" (Allen 1940:864).

Taxonomy. The common Sichuan vole was described as a member of *Microtus* and consistently treated as such until 1990 when it was classified in the newly established *Volemys* (Zagorodnyuk 1990). Ellerman (1941) treated *millicens* as the sole member of the *millicens* species group within *Microtus*. Allen (1940) saw *millicens* as representing "a smaller form of [*Neodon*] *clarkei*" and in the past these species were indeed occasionally confused. *N. clarkei* has a longer tail (TL=55–67 mm vs 42–53 mm in *millicens*) and ridged skull (smooth in *millicens*). Triangles T6–7 on M_1 are integrated into AC in *millicens*; in *clarkei*, T6–T7 are separated though not isolated from AC by re-entrant angles LR5 and BR4 (Figure 180a').

Distribution (Figure 181). The relatively small range of *millicens* (area=97,720 km^2) is in two fragments, in north-eastern Sichuan and south-western Xizang. These fragments are far apart and *musseri* occurs in-between. There is one report of *millicens* from Yunnan (Zhang et al. 1997) which was not accepted by Luo et al. (2000) or Wang (2003), questioned in Musser & Carleton (2005) but still quoted in Jiang et al. (2015); we did not plot it on the map (Figure 181). The common Sichuan vole occupies forests (evergreen broadleaf and alpine coniferous) and alpine meadows (Luo et al. 2000) at 1,240–3,750 m a.s.l.

Characteristics. Slightly smaller than *musseri* and with a proportionally shorter tail (TL/H&B=0.39–0.60). Dimensions: BWt=20–38 g, H&B=85–115 mm, TL=42–52 mm, HF=16–22 mm, EL=12–16 mm, CbL=22.3–27.8 mm, ZgW=12.3–15.8 mm, MxT=5.1–

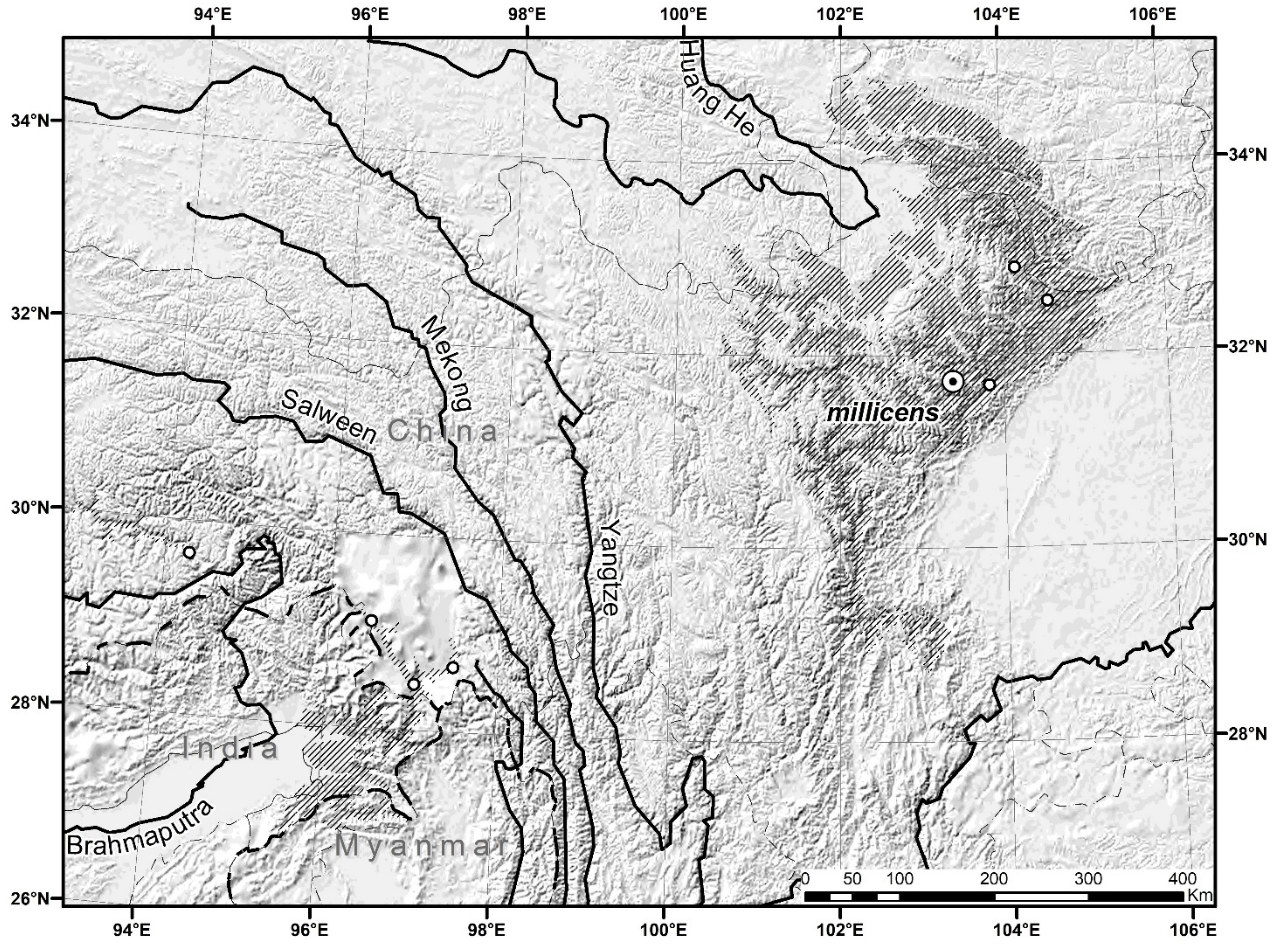


Figure 181: Distributional range of the common Sichuan vole *Volemys millicens*.

6.3 mm. Fur is long (~12 mm), soft and loose, dark-brown above and gradually turning into smoke-grey underside; hair bases are slate throughout. The tail is sharply bi-coloured, dark brown-grey above, light-grey below; it is fully clad with stiff hairs which hide the underlying annulation and terminate to a moderately long pencil. Ears are greyish-brown and paws vary from greyish-white to greyish-brown. Plantar pads are similar to those in *Neodon sikimensis* and *leucurus*. The sole is hairy behind the pads; of the metatarsal pads, the medial is large and the lateral is much smaller (Figure 179). Glans penis is short (3.3–4.6 mm) and narrow (1.7–2.0 mm). Baculum is of trident type; the proximal stalk (length=2.3–2.5 mm) has a widely rhomboid basal expansion (width=1.2–1.6 mm). Central distal baculum is short (1.0–1.2 mm) and heavy (width=0.48–0.60 mm); lateral digits are narrow and comparatively long (0.7–0.9 mm; Liu et al. 2017). The skull is slightly narrower than in *musseri* (ZgW/CbL=0.55–0.56). The nasals are longer, the orbital constriction is wider (3.9–4.7 mm), incisive foramina are shorter and the bullae are smaller. The medial spine on the posterior bony palate is wide and low and the lateral pits are very shallow. Foramina on the allisphaenoid are large. The articular process of the mandible is long and robust (Figure 176). M^2 has an additional postero-lingual triangle T5 which opens medially into T4. M^3 consists of 3–4 inner and 3 outer salient angles; triangles T2–T3 are either confluent or alternate; the posterior cap is of variable length. M_1 has 4 alternating triangles (T1–T4); T5 usually communicates with the triangular anterior cap (AC).

Variation and subspecies. Monotypic. The unnamed "Zayü form" of *millicens* from southern Zayu (Xizang) and reported in Wang (2003) in reality represents *Neodon medogensis* (Liu et al. 2017).

Volemys musseri (Lawrence, 1982) – Marie's Sichuan Vole

Microtus musseri Lawrence, 1982: 6. Type locality: "Chen Lliang Shan range, 30 miles [48km] west of Wenchuan", Sichuan, China, 2,745 m above sea level.

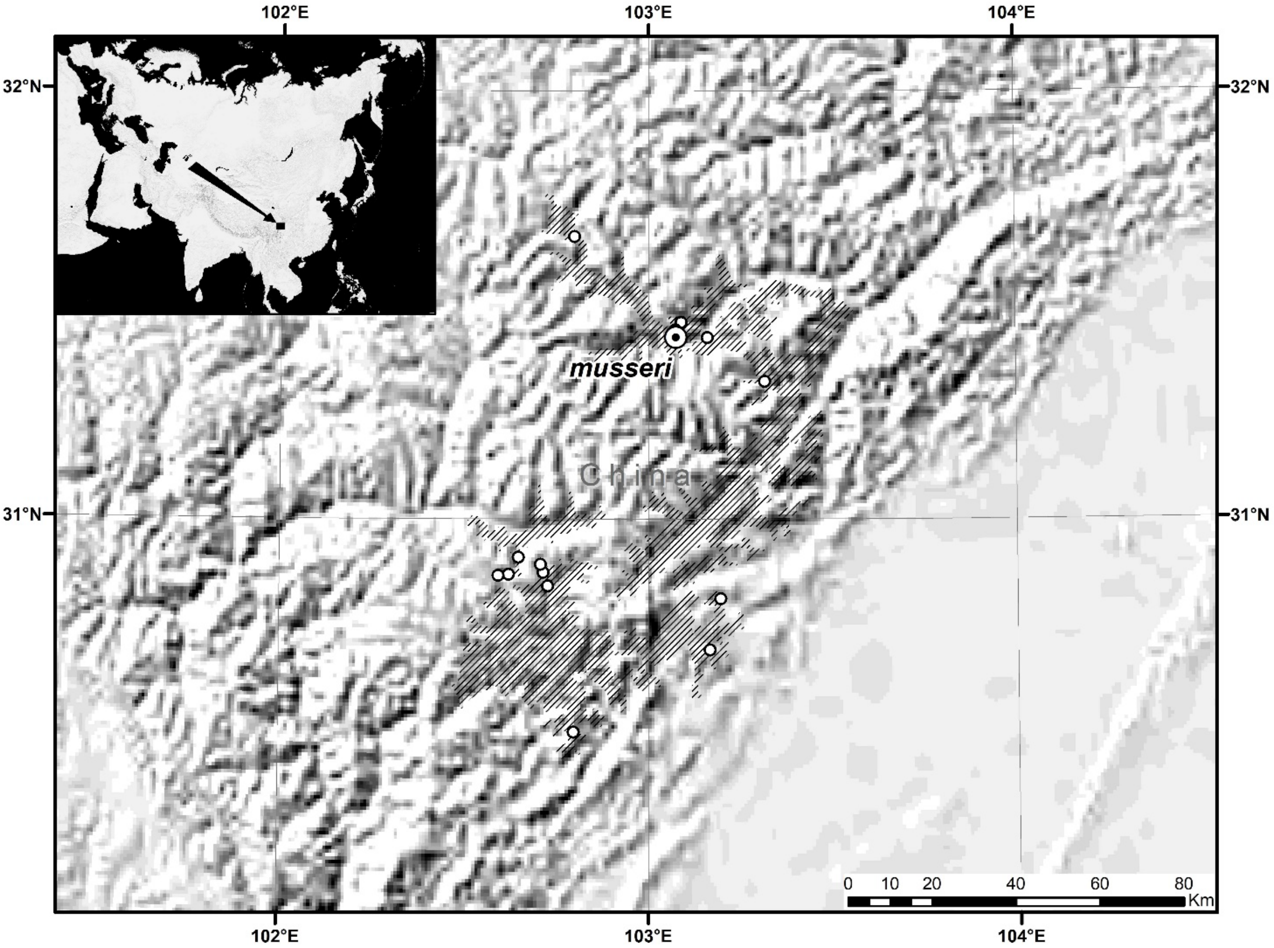


Figure 182: Distributional range of Marie's Sichuan vole *Volemys musseri*.

Distribution (Figure 182) The extremely small range (area=3,410 km^2) is situated at high altitudes (2,320–3,660 m) in the Qionglai and Jiajin mountains, Sichuan (southern China). Lives among rocks in alpine meadows.

Characteristics. A vole of medium size and with a proportionally long tail (TL/H&B=58–70). Dimensions: H&B=90–129 mm, TL=47–72 mm, HF=18–23 mm, EL=15–18 mm, CbL=26.6–28.2 mm, ZgW=13.6–16.0 mm, MxT=5.5–6.7 mm. Fur is soft and long (~12 mm) and the ears barely protrude. Dorsal pelage is dark brown, slightly grizzled by black and buffy hair tips; ventral side is slate and shaded light buff; the transition on the flanks is gradual. The tail is uniformly dark-brown to bi-chromatic (dark brown above, dirty whitish or buff below); it is densely covered by stiff hairs which cover the annulation. Feet are greyish-brown or drab. The glans penis is rather long (4.75–5.40 mm) and moderately thick (width=2.67–2.80 mm). Baculum is of trident morphology; the stick-shaped proximal baculum (length=2.82–3.10 mm) has a moderately expanded base (width=1.30–1.40 mm). The distal central baculum (length=1.58–1.60 mm) accounts for >½ the length of the proximal bone; lateral digits are also long (1.30–1.33 mm; Liu et al. 2007). The skull is shallow (height behind M^3/CbL=0.30–0.32), with a flat dorsal profile; zygomatic arches are moderately expanded (ZgW/CbL=0.55–0.58), braincase is long and orbital constriction is wide (3.5–4.5 mm). The nasals terminate before reaching the front level of the incisors. The incisive foramina are long, the palatal grooves are deep, the medium septum at the end of the palate is broad and low and the lateral pits are correspondingly shallow. Bullae are moderately large. The mandible is low with long, slender articular and angular processes; there is no trace of an alveolar bulge (Figure 176). Incisors are orthodont. M^1 and M^2 are highly characteristic in having an additional posterolingual triangle T5 (Figure 180d). M^3 has 4 inner and 3 outer salient angles and the postero-lingual salient angle LS5 is invariably small; T4 is either closed (75% of cases) or confluent with the heel. On M$_1$, triangles T1–T2 alternate while T3–T4 are confluent in ~20% of individuals. T5–T6 open into the AC which has an additional salient angle (LS5) anterior to T5 (Lawrence 1982).

Variation and subspecies. A monotypic species.

GENUS: *Neodon* Hodgson, 1849 – Scrub Voles

Taxonomy. The current concept and scope of *Neodon* is the product of molecular phylogenetic analyses done during the last decade (Liu et al. 2012b, 2017, Steppan & Schenk 2017, Pradhan et al. 2019). Prior to this, scrub voles were classified in different genera. *Neodon* contained *sikimensis* and the *irene* species group, *leucurus* was frequently in *Phaiomys*, *clarkei* in *Microtus* or *Volemys*, and *fuscus* in *Lasiopodomys*. Furthermore, *Neodon* typically also contained *yuldaschi*, which is now in the subgenus *Blanfordimys*. Based on Pradhan et al. (2019), we divide *Neodon* to 2 subgenera; the subgenus *Phaiomys* is further split into 3 species groups. Phylogenetic reconstruction based on the complete *Mt*-genome retrieved a chaining hierarchy among the 7 species of scrub voles (Fan et al. 2011a, Li et al. 2019) and therefore does not support the infrageneric classification as proposed below.

Neodon was initially accepted as a full genus (Horsfield 1851, Jerdon 1867), later ranked as a section of *Arvicola* (Blanford 1881b, Sclater 1891) and for the majority of the 20th century was synonymised with *Microtus or Pitymys*. Zagorodnyuk (1990) reinstalled *Neodon* as a genus in its own right, which gradually gained support and is now widely agreed upon.

Neodon, regardless of its rank, was uniformly viewed as representing the Asiatic counterpart to the European *Terricola* (Hinton 1926a, Chaline et al. 1999) and alongside *Phaiomys*, was thought to be a direct survivor of an early radiation from the Lower Pleistocene (Hoffmanv & Koeppl 1985). Chaline & Mein (1979) claimed *Phaiomys* to be a direct descendant of *Allophaiomys* and Zakrzewski (1985) found no distinction of generic value in the molar pattern between *Allophaiomys* and *Neodon*. In a similar matter, Nadachowski & Zagorodnyuk (1996) stressed the similarities between *Neodon, Phaiomys, Blanfordimys*, and the fossil *Allophaiomys*, but Robovský et al. (2008) suggested that the presumably archaic dentition of these taxa may have evolved secondarily. Martin (1969) believed *Neodon* to be Holarctic in distribution. Molecular phylogenetic reconstructions retrieved close relationships between *Neodon*, *Alexandromys* and *Lasiopodomys* (Steppan & Schenk 2017, Li et al. 2019).

Over the last years, the number of species in *Neodon* has changed more profoundly than in any other comparable arvicoline group with 4 new species being added since 2012 to the previous 6 species. Interspecific genetic distances in the genus are generally high (11.1–14.4%; Pradhan et al. 2019).

Distribution. Himalayan slopes in Nepal, Sikkim and Bhutan, and the western, eastern and southern fringes of the Quinghai-Tibet plateau in China, northern India, and northern Myanmar. Scrub voles occupy high altitude forests, scrubland and pastures.

Characteristics. In its narrow sense, *Neodon* was defined as combining pitymoid M_1 (broadly confluent triangles T4–T5) with the overall morphology of *Microtus* (Hinton 1926a, Allen 1940). The subsequent incorporation of additional species dissolved the morphological consistency of the genus, which is at present definable only by molecular markers.

Scrub voles are small to moderately large arvicolines with a relatively long tail (TL/H&B≈035–0.50) which is usually well-clothed with hair. Flank-glands are present in males. The fur is soft and long but less velvety than in *Terricola*; some species lack the longer and stiffer hairs. Ears are moderately long and normally protrude above the fur; antitragus is distinct but low. Claws on front and hind feet are rather long and of approximately the same length. There are 5–6 plantar pads (Figure 183) and 8 (rarely 6) nipples. Skull is of a *Microtus*-type; the temporal ridges normally fuse to form a shallow interorbital crest; several species have a depression on the anterior frontals between the posterior edge of the nasals and the diverging temporal ridges. Zygomatic arches are moderately to widely expanded (ZgW/CbL=0.55–0.68) and braincase is low to deep. The spongy bone inside the bullae is weakly developed. Incisors are predominantly orthodont, rarely proodont. Molars deviate from *Microtus* by having, at least in some species, additional posterior salient loops on M^1–M^2. The M_1 is frequently pitymoid and in some species (e.g. *sikimensis* and the *clarkei* species group) displays 2 sets of confluent triangles formed by T4–T5 and T6–T7. Triangles T3–T4 on M^2 are frequently confluent. The glans penis is of a simple cylindrical shape with a ventral furrow and blunt tip; the baculum is of trident morphology and the lateral distal digits are frequently poorly ossified or remain cartilaginous. The sex chromosomes are synaptic and therefore undergo XY chromosome pairing in the males (reported for *N. nepalensis*; Mekada et al. 2002).

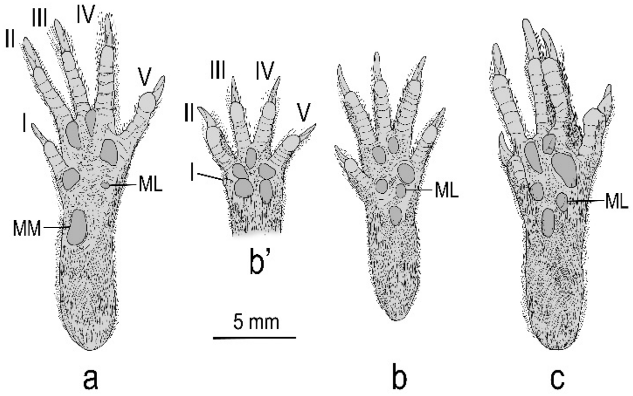


Figure 183: Left sole (a–c) and palm (b') in scrub voles *Neodon*: a–*N. sikimensis* (Makalu, Nepal); b– *N. irene* (Lianhuashan, Gansu, China); c– *N. fuscus* (north-eastern Tibet, China).

Key to species

1a) M^3 with 2 re-entrant angles on each side and with a short and simple posterior cap ………....................... 2
1b) M^3 normally with 3–4 inner re-entrant angles; the posterior cap is usually long and complex ……..…… 4
2a) Dorsal pelage is black-brown, paws are dark; T5 on M_1 and the anterior cap are isolated ……………………………………......…… *linzhiensis*
2b) Dorsal pelage is lighter (never black-brown), paws are light; T5 on M_1 is confluent with the anterior cap ……………………………………………..............3
3a) M_1 with confluent triangles T3–T4; fur in the auricular region does not contrast the dorsal pelage; tail longer (TL/H&B>0.30); glans penis is shorter (<4.6 mm) and narrower (≤2.8 mm); lateral distal baculum is cartilaginous; skull is wider (ZgW/CbL>0.61); mandibular body is deep, angular process is robust ………………………….....……………… *leucurus*
3b) M_1 with alternating triangles T3-T4; light fur in the auricular region contrasts the dark dorsal pelage; tail shorter (TL/H&B<0.30); glans penis is longer (>4.7 mm) and thicker (≥2.8 mm); lateral distal baculum is slightly ossified; skull is narrower (ZgW/CbL<0.62); mandibular body is shallow, angular process is slender …………………………………………..………… *fuscus*

4a) T6 of M_1 is normally developed; M^2 with an additional postero-lingual salient angle LS4 (T5) 5

4b) T6 of M_1 is obtuse or absent 8

5a) M^1 with an additional postero-lingual salient angle LS4 (T5) .... *nyalamensis*

5b) M^1 without additional postero-lingual salient angle LS4 (T5) 6

6a) Proximal baculum long (>3.0 mm) with a wide base (≥1.9 mm or more); present in the trans-Himalayan range (mainly to the south of the Yarlung Tsangpo River) .... *sikimensis*

6b) Proximal baculum short (<3.0 mm) with a narrower base (≤1.8 mm); present to the north of the Yarlung Tsangpo River 7

7a) Dorsal pelage dark brown; 5 plantar pads; proximal baculum longer (>2.60 mm), distal baculum is cartilaginous .... *clarkei*

7b) Dorsal pelage blackish brown; 6 plantar pads; proximal baculum shorter (<2.60 mm), distal baculum is ossified .... *medogensis*

8a) Native to western Nepal; M^2 occasionally with an additional postero-lingual salient angle LS4 (T5) .... *nepalensis*

8b) Native to China and Myanmar; M^2 without additional postero-lingual salient angle LS4 (T5) 9

9a) Smaller: MxT usually <6.0 mm; adult skull smooth; temporal ridges absent from the parietals.............. *irene*

9b) Larger: MxT usually >6.0 mm; adult skull ridged; temporal ridges extend to the parietals .... *forresti*

SUBGENUS: *Nedon* Hodgson, 1849 – Himalayan Scrub Voles

Neodon Hodgson, 1849 (in Horsfield 1849:203). Type species by monotypy is *Neodon sikimensis* Hodgson.

Synonyms. *Bicunedens* Hodgson, 1863 [nomen oblitum].

Taxonomy. Sister position of *Neodon* s.str. against *Phaiomys* is evident from *Mt*-phylogenetic trees (Pradhan et al. 2019).

Distribution. The trans-Himalayan parts of Nepal, Sikkim, Bhutan and southern Xizang (China). Restricted to high altitude forests, scrubland and pastures.

Characteristics. Moderately large scrub voles with ferruginous-brown dorsal pelage. Females have 6–8 nipples. The skull is strongly built with moderately expanded zygomatic arches (ZgW/CbL=0.57–0.62); braincase is comparatively short and rather shallow. Bullae are small; temporal ridges form the interorbital crest (Figure 184). M^2 frequently has additional postero-lingual loop LSA4; M^3 is usually complex with up to 4 inner and 3–5 outer salient angles (Figure 185).

Neodon sikimensis Hodgson, 1849 – Sikkim Scrub Vole

Neodon Sikimensis Hodgson, 1849 (in Horsfield 1849:203). Type locality "Sikim" as subsequently designated in Horsfield (1851:146), restricted to "Sikkim, near Darjeeling" (Pradhan et al. 2019:18). This designation is in agreement with Jerdon (1867:217) who claimed the species "has only been procured in Sikim, near Darjeeling, at heights varying from 7,000 to 15,000 feet [=2,135–4,270 m]". Similarly, Blanford (1881b:114) states "All Mr. Hodgson's specimens appear to have been obtained in Darjiling itself or the immediate vicinity of the station." Furthermore, in 1860 the Museum of the Asiatic Society of Bengal was in possession of a voucher from "Dorjiling" (=Darjeeling) (Blyth 1863b:125). For the authority and the year see the account on taxonomy below.

Synonyms. *Arvicola thricolis* Hodgson, 1863 [nomen nudum]; *Arvicola nigrescens* Hodgson, 1863 [nomen nudum]; *Bicunedens perfuscus* Hodgson, 1863 [nomen nudum]; *Arvicola thricotis* Jerdon, 1867 [emendation of *thricolis* Hodgson].

Taxonomy and nomenclature. During the mid to late 20th century, *sikimensis* also included *irene* and *forresti*; see under that species. For recent taxonomic changes see comments on *nepalensis*.

Kaneko & Smeenk (1996) claimed that *sikimensis* Hodgson is a nomen nudum, and that the correct authority is Horsfield, with 1851 as the year of publication. We argue for the established use of the taxonomic authority. Firstly, under the provision of Declaration 32 (ICZN 1957), the author of the name is

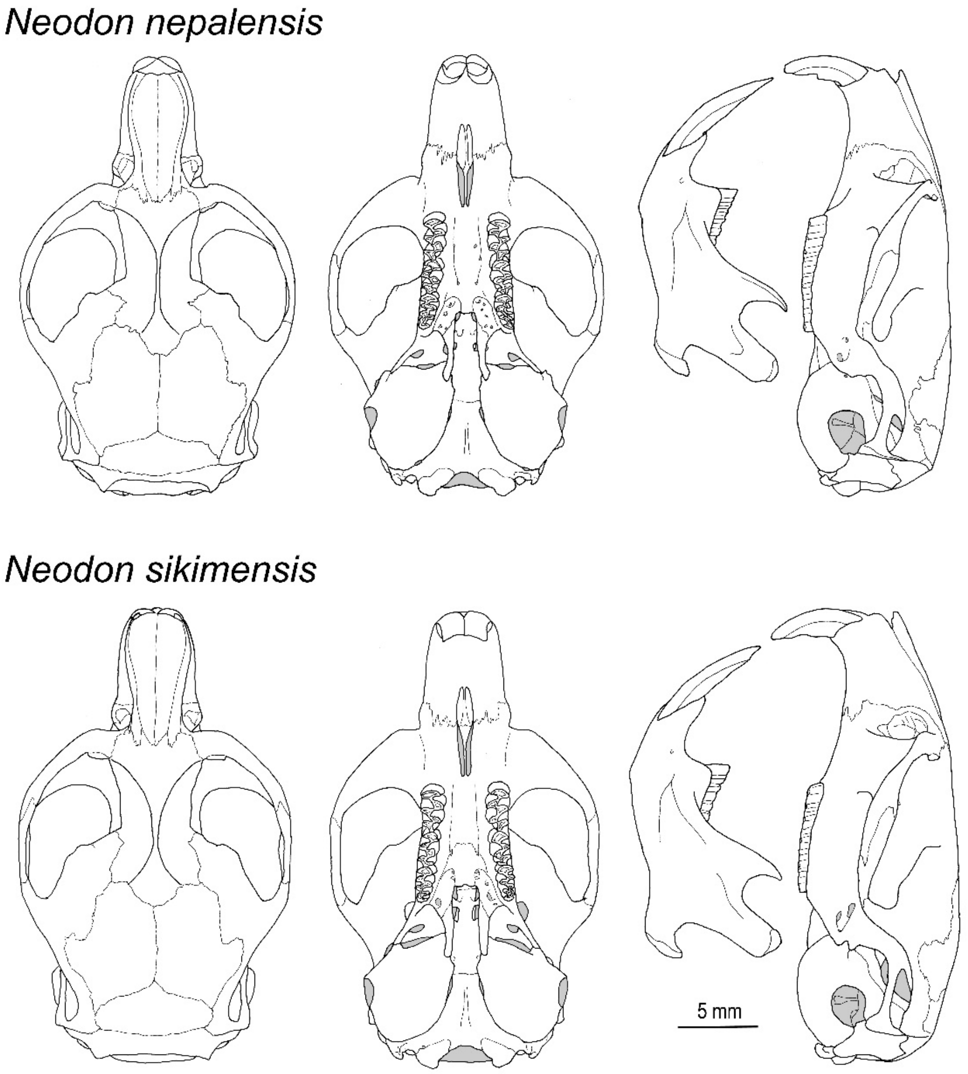


Figure 184: Skull in scrub voles from the subgenus *Neodon* (top-to-bottom): *N. nepalensis* (top–Uttar Ganga, Nepal) and *N. sikimensis* (bottom–Ghum, Darjeeling Municipality, India).

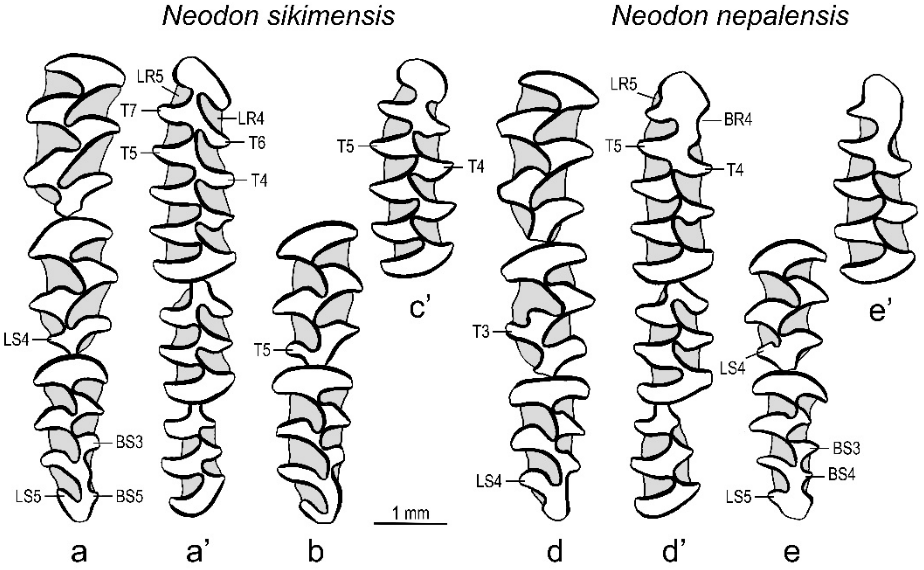


Figure 185: Molar pattern in voles from the subgenus *Neodon*. *Neodon sikimensis*: upper (a) and lower row (a'–Makalu, Nepal); isolated M^{2-3} (b–Garesh Hima, Sontag, Nepal) and M_1 (c'–Ghum, Darjeeling Municipality, India). *N. nepalensis*: upper (d) and lower row (d'– Thakkhola, Nepal); isolated M^{2-3} (e) and M_1 (e'–Dhopatan, Nepal).

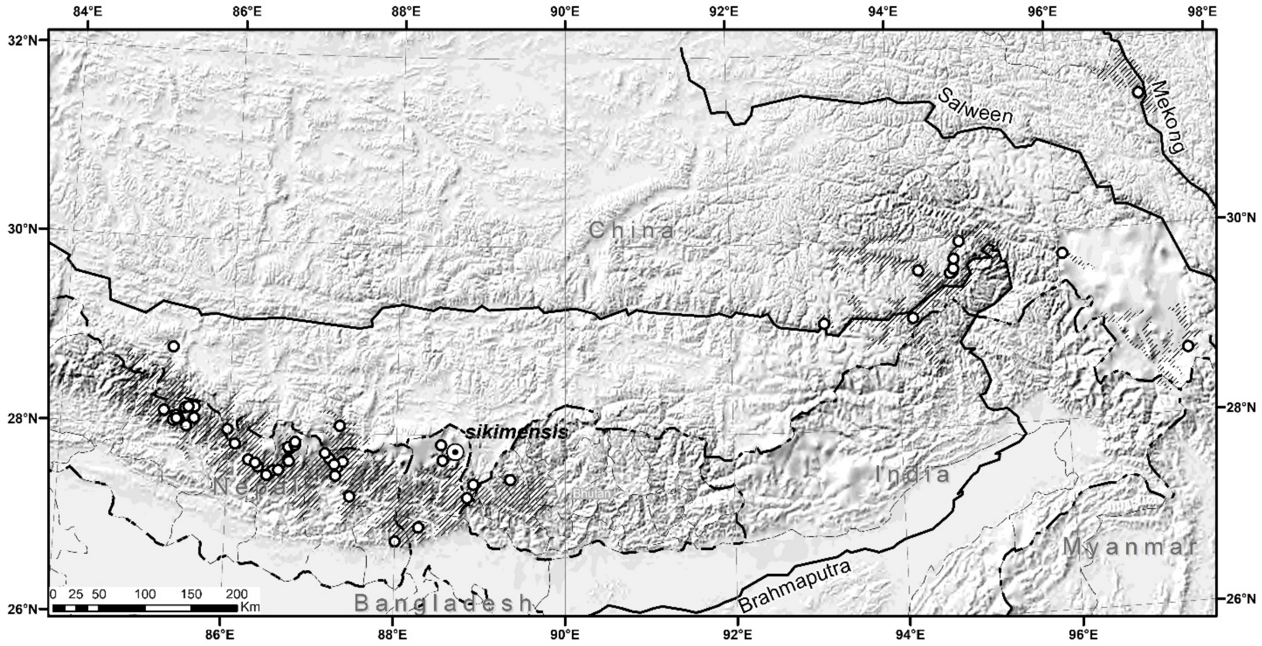


Figure 186: Distributional range of the Sikkim scrub vole *Neodon sikimensis*.

the zoologist who proposed the name (in this case Hodgson) and not the author of the report (Horsfield). Publication of *sikimensis* (in Horsfield 1849) contains a comparison with other voles ("in many respects allied to *Arvicola*"; "appears to be nearly allied to *Arvicola Roylei*, Gray") and a somewhat rudimentary diagnosis: "There are, however, in the *Neodon* [*sikimensis*] some differences in the folds of the upper and lower grinders". The "other distinguishing characters … will be pointed out in Mr. Hodgson's detailed description" (Horsfield l. c.) which, however, never materialised.

The name combination *Neodon sikimensis* Hodgson, 1849 was widely accepted during the 2nd half of the 19th century (Gray 1863, Jerdon 1867, 1874, Blanford 1891, Sclater 1891) and beyond (Pearch 2011:104), never involving any sort of taxonomic confusion.

Distribution (Figure 186). The Eastern Himalayan eco-region (Pradhan et al. 2019) to the west of the Mekong River: southern, south-eastern and eastern Xizang (as west as Jilong Co. at the 85.29th meridian; China), Sikkim and West Bengal (India), Bhutan (known from a single locality; Zhang et al. 1997), and eastern Nepal (as far west as Somtang). Geographic range consists of 1 large fragment (in eastern Nepal, Sikkim West Bengal, Bhutan and southern Xizang, China) and 6 small isolates in south-eastern Xizang (China),: (i) Jilong County, (ii) Lang Xian, (iii) Milin and Linzhi Counties, (iv) Bomi County, (v) Chayu County, and (vi) Changdu County.

The entire range covers an estimated 40,960 km^2. Lives in meadows, stony walls surrounding small fields, rhododendron scrubs, forest edges and the interior of dense mountain forests between 1,415 and 5,070 m a.s.l.; also recorded above the tree-line (Gregori & Petrov 1976, Agrawal 2000, Daniel 2015).

Characteristics. Moderately large scrub vole with proportionally long tail (TL/H&B=0.31–0.50). Dimensions: BWt=21–50 g, H&B=97–123 mm, TL=34–57 mm, HF=16–22 mm, EL=10–16 mm, CbL=24.4–28.5 mm, ZgW=13.0–17.0 mm, MxT=6.0–7.7 mm. The tail is densely clad with short, stiff hairs which usually conceal the annulation; terminal pencil is short (=2–2.5 mm). Ears are rounded, thinly covered with short brown hair and overtop fur for ~½ their length. Feet are slender and densely hairy above, almost naked below. The front thumb has a short claw; the remaining claws are modestly long and compressed. There are 5 large palmar and 6 plantar pads; the lateral metatarsal pad is tiny and absent in some individuals; the medial metatarsal pad is large and elongated (Figure 183a). Fur is soft and long (9–10.5 mm), intermixed with longer black-tipped hairs (length=13.5–14.5 mm). Dorsal side varies from deep brownish-black, minutely interspersed with yellow to dark ferruginous-brown hair tips; flanks are less rusty; the underside is slate-grey with a slight rusty or fulvous shade, and grizzled with white-tipped hairs. Feet are brown; tail is indistinctly bi-coloured, blackish-grey above, slightly lighter below. Females have 8 (Mitchell 1977) or 6 nipples (Ellerman 1961). Baculum is of trident type; proximal bone is 3.0–3.5 mm long and 1.9–2.0 mm wide across the expanded base. The central digit (length=1.0–1.2 mm) is ~36% the length of the basal bone. The lateral digits (length=0.6–0.8 mm) are well-ossified (Gregori & Petrov 1976, Liu et al. 2012b).

Skull shows no peculiarities (Figure 184). The upper incisors are more orthodont than in *nepalensis* and the alveolar process on the mandible is less prominent. Molars resemble the pattern in the *clarkei* species group. In the vast majority of cases, the M_2 has an additional lingual salient angle (LS4) which may assume the form of a triangle T5; a similar loop is also occasionally present on M^1. The M^3 is complex with 4 lingual and 3–5 labial salient angles; noteworthy, BS4 is frequently more vestigial than BS5. M_1 with 2 sets of confluent triangles (i.e. T4–T5 and T6–T7) which are mutually isolated by deep re-entrant angles LR4 and BR3; T4–T5 occasionally alternate (Figure 185c'). Re-entrant angles LR5 and BR4 are frequently deep enough to isolate the AC.

Variation and subspecies. Enamel pattern of M_1 and M^3 is more complex in Nepal than in Tibet and Sikkim (Pradhan et al. 2019:18). At present, *sikimensis* is considered to be monotypic.

Neodon nepalensis Pradhan, Sharma, Sherchan, Chhetri, Shrestha & Kilpatrick, 2019 – Nepalese Scrub Vole

Neodon nepalensis Pradhan, Sharma, Sherchan, Chhetri, Shrestha & Kilpatrick, 2019:18. Type locality: "Nepal, Dolpo District, Dhorpatan, 8,950 ft [2,730 m] (UTM R44-703810-3159902; N 28°33' E 83°05')."

Taxonomy. Until recently, *nepalensis* was not formally distinguished from *sikimensis*. Nadachowski & Zagorodnyuk (1996) were perhaps the first to realise, on the grounds of dental variation, that *sikimensis* is a species complex. This view was confirmed in the *Mt-*

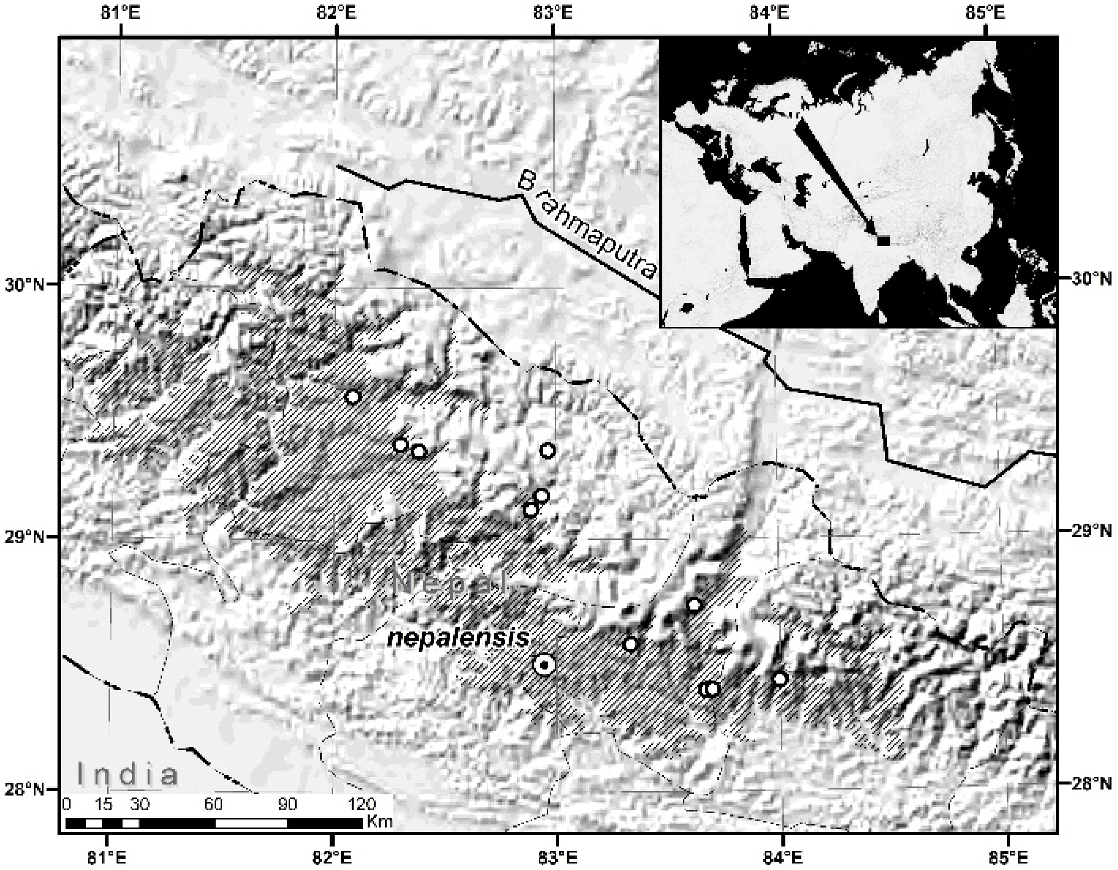


Figure 187: Distributional range of the Nepalese scrub vole *Neodon nepalensis*.

phylogenetic study by Liu et al. (2012b). Pradhan et al. (2019) provided a formal description and naming of the new species.

Distribution (Figure 187). The Western Himalayan eco-region, to the west of the Daraudi River in Madhya Pashchimanchal and Pashchimanchal (western Nepal). The entire range is estimated at 20,653 km^2. Lives on high altitudinal (2,200–4,400 m a.s.l.) meadows, rhododendron shrublands, and temperate forests (Mitchell 1977, Pradhan et al. 2019). Allopatric with respect to *sikimensis*.

Characteristics. Dimensions: BWt=20–37 g, H&B=91–112 mm, TL=26–44 mm, HF=15–18 mm, EL=8–12.5 mm, CbL=24.7–27.3 mm, ZgW=14.8–16.5 mm, MxT=6.0–7.2 mm. Smaller than *sikimensis* with a proportionally shorter tail (TL/H&B=0.36–0.45). Colouration is similar: back is buffy-brown to intensely ferruginous-brown; flanks are lighter and more fulvous and the underside is slate-grey with a slight fulvous shade. Feet and ears are brown; tail is indistinctly bi-coloured, blackish-grey above, slightly lighter below. Females have 8 nipples. Skull shows no peculiarities (Figure 184). The upper incisors are more proodont than in *sikimsensis* and the alveolar process in the mandible is more prominent. The M^2 is either with or without the postero-lingual salient angle LS4; M^3 usually with 3 salient angles on either side but there can be 4 inner and up to 5 outer salient angles. M$_1$ with a single set of confluent triangles (i.e. T4–T5) which open into the dental field consisting of T6 (which is obtuse or absent), T7 and AC. Re-entrant angles LR5 and BR4 are shallow and BR4 is frequently missing. Karyotype (reported as *sikimensis*; Mekada et al. 2002): 2n=48, NF$_a$=56; 5 autosomal pairs are bi-armed (meta-, submeta- and subtelocentric) and 18 pairs are acrocentrics of variable size. The X is metacentric and the Y is telocentric.

SUBGENUS: *Phaiomys* Blyth, 1862 – Thibetan Scrub Voles

Phaiomys Blyth, 1862 (in Theobald 1862:519). Detailed description provided in Blyth (1863a:89). Type species by monotypy is *Phaiomys leucurus,* Blyth. For the year of publication see under *Neodon leucurus*.

Taxonomy. In the past *Phaiomys* was usually defined as a monospecific group for *leucurus*, and was ranked as a genus in its own right or a subgenus of either *Microtus* or *Pitymys*. Since the 1970s, Russian authors have classified *Phaiomys* as a synonym of *Neodon* or its subgenus (e.g. Gromov & Polyakov 1977. This was opposed by Repenning (1992a) but gained support due to molecular phylogenetics (e.g. Steppan & Schenk 2017). For the past use of *Phaiomys* in relation to *Blanfordimys* and the fossil *Allophaiomys*, see under *Blanfordimys*.

Our division of *Phaiomy* into 3 species groups largely follows Pradhan et al. (2019).

Distribution. North of the trans-Himalayan area on the western, eastern and southern slopes of the Quinghai-Tibet plateau in China, northern India, and very marginally Nepal and northern Myanmar. In south-eastern Xizang the ranges of *Phaiomys* and *Neodon* s.str. partly overlap.

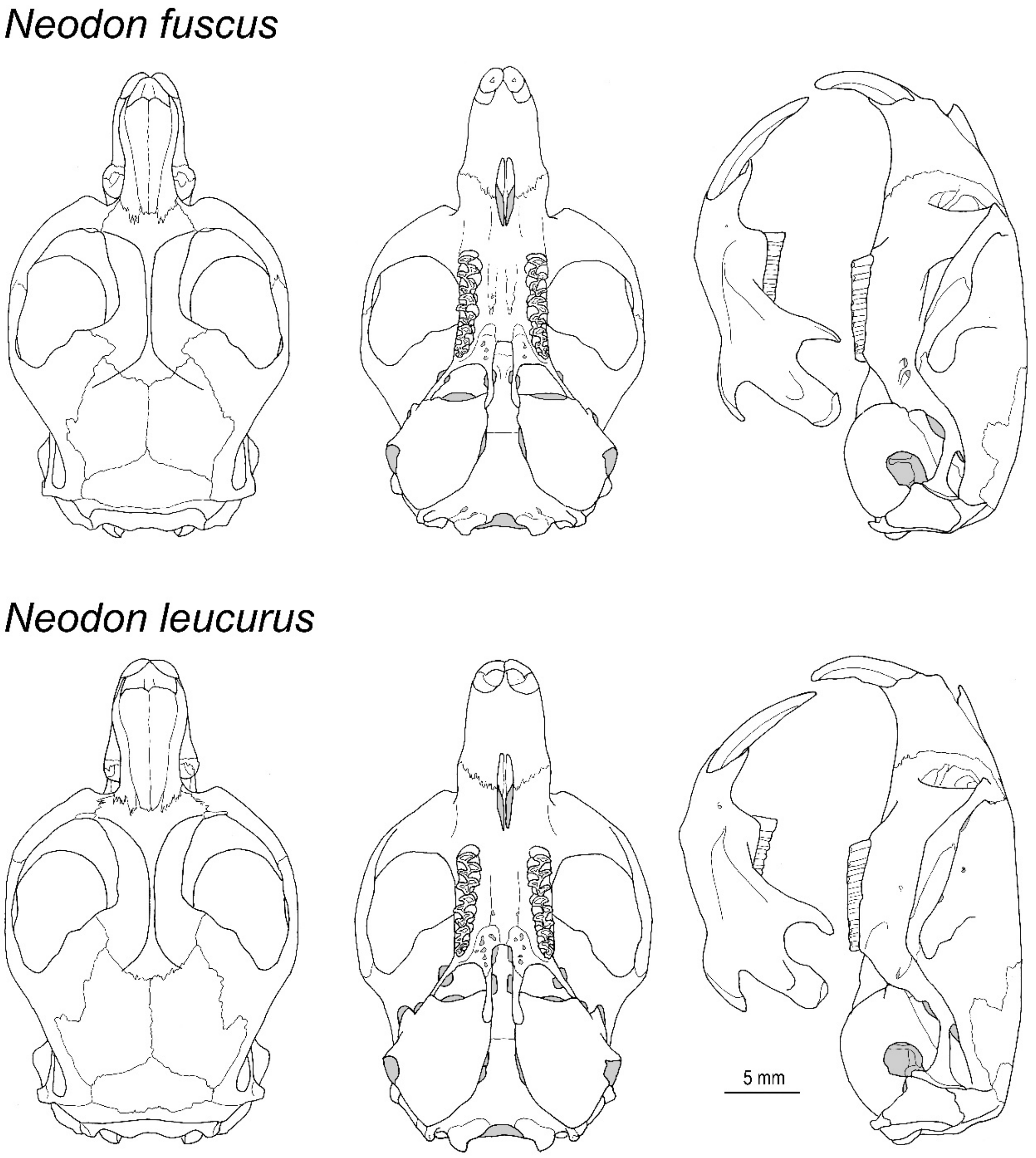
Characteristic. *Phaiomys* is a diverse assemblage of 8 species and is morphologically indefinable.

Species group *leucurus*

Taxonomy. In the past the 2 species in this group (*leucurus* and *fuscus*) were allocated to different genera, most commonly to *Microtus* (*leucurus*) and *Lasiopodomys* (*fuscus*; e.g. Musser & Carleton 2005). Such a view resulted from the over-valued taxonomic significance of the M$_1$ morphology. In the *Mt*-phylogenetic tree the *leucurus* group assumes a sister position against the *irene* species group (Liu et al. 2017, Pradhan et al. 2019).

Distribution. This species group occupies nearly the entire range of the subgenus except its easternmost parts. The range of *fuscus* is categorically smaller than that of *leucurus*, being almost entirely inside the range of the latter. The two species are partially sympatric.

Characteristics. Large, heavily built and short-tailed (TL/H&B<0.32) scrub voles. The ears do not extend much beyond the hair; they are clad by short hairs. Front thumb usually with a minute claw; claws on front and hind toes prominent and slightly enlarged. Soles are hairy posterior to metatarsal pads (Figure 183c). Fur is



Neodon fuscus

Neodon leucurus

Figure 188: Skull in scrub voles from the *leucurus* species group, subgenus *Phaiomys* (top to bottom): *N. fuscus* (Orin-nor, north-eastern Tibet, China; top) and *N. leucurus* (Tibet Autonomous Region, China; bottom).

thick, soft and long (9–10.5 mm; longer protruding hairs measure 10–12 mm). The tail is densely clad with stiff hairs which terminate to a pencil (length=3–5 mm). There are 5 plantar and 6 palmar pads (Figure 183c); ~⅓ of individual *leucurus* have 5 plantar pads (cf. Miller 1899a). Females have 8 nipples. The skull is deep, with proodont upper incisors; zygomatic arches are heavy and widely expanded. Nasals are short, wider anteriorly than posteriorly; they terminate far behind the frontal plane of the upper incisors. The skull is well-ridged with a prominent sagittal crest. Bullae are moderately large; incisive foramina are short (Figure 188). Lateral pits at the posterior edge of the palate are deep. Alveolar process on the mandible is distinct to prominent. Enamel pattern is highly characteristic: M^3 has 2 re-entrant angles on each side. M$_1$ has 3–4 closed triangles; the antero-lingual triangle T5 is confluent with AC and there are only 3 re-entrant angles on the outer side; the antero-lingual re-entrant angle LR5 is shallow and usually absent (Figure 189). The lateral distal baculum is weakly ossified or remains cartilaginous.

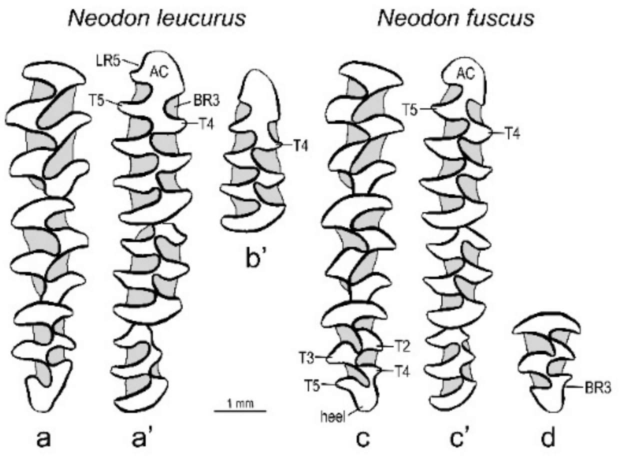


Figure 189: Molar pattern in voles from the *leucurus* species group, subgenus *Phaiomys*. *Neodon leucurus*: upper (a) and lower row (a'; Lhasa, Xizang, China); b'–isolated M_1 (Tibet Autonomous Region, China). *N. fuscus*: upper (c) and lower row (c'; Toso-Nur, Qinghai, China); d–isolated M^3 (Dy-Chyu river, E Tibet, China).

Neodon leucurus (Blyth, 1862) – Blyth's Scrub Vole

Phaiomys leucurus Blyth, 1862 (in Theobald 1862:519). Type locality by subsequent designation (Blyth, 1863a:89): "near Lake Chomoriri [Tsho-marari]", Rupshu Province, Jammu and Kashmir, northern India.

Synonyms. *Arvicola Blythi* Blanford, 1875 [new name for *Phaiomys leucurus* Blyth]; *Microtus strauchi* Büchner, 1889; *Microtus tsaidamensis* Satunin, 1903; *Microtus (Phacomys) waltoni* Bonhote, 1905; *Microtus (Phaiomys) waltoni petulans*, Wroughton, 1911; *Phaiomys everesti* Thomas & Hinton, 1922; *Pitymys (Phaiomys) leucurus zadoensis* Zheng & Wang, 1980.

Nomenclature. The name *Phaiomys leucurus* was used for the first time in Theobald (1862:519) who "gave a recognizable description […] and wanted to associate the authorship to Blyth." (Roonwal, in Ellerman 1961:469). Roonwal (*l.c.*) therefore quotes 1862 (and not 1863) as the correct year of publication for *leucurus*.

Distribution (Figure 190). Blyth's scrub vole has the largest, although extremely fragmented, distribution in the genus (area=420,130 km^2). The vole is present along the entire periphery of the Quinghai-Tibet plateau except for the northern rim; it is present in China (Qinghai, Xizang, and marginally southern Xinjiang), Jammu and Kashmir (northern India), and very peripherally in north-central Nepal (Mustang District, Pashchimanchal). Lives in alpine desert and arid high mountain steppes, aggregating in stream beds and river banks, around lakes and in marshy spots at elevations of

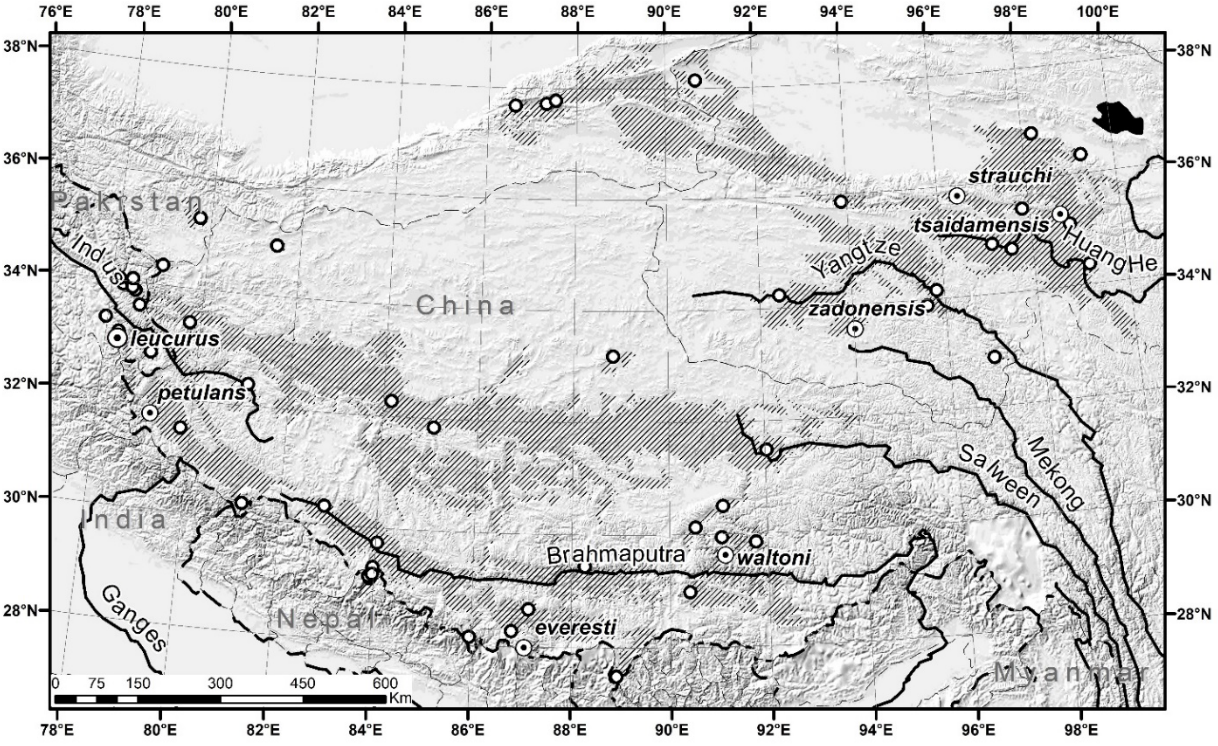


Figure 190: Distributional range of Blyth's scrub vole *Neodon leucurus*.

2,860–5,270 m (Chakraborty 1983, Agrawal 2000, Hu et al. 2014).

Characteristics. Dimensions: BWt=20–65 g, H&B=87–130 mm, TL=21–47 mm, HF=15–22 mm, EL=9–15 mm, CbL=24.5–30.0 mm, ZgW=15.0–19.2 mm, MxT=5.6–7.9 mm. Size is large, only slightly smaller than in *N. fuscus*, the tail is comparatively longer (TL/H&B=0.29–0.32) and ears on average larger. Colouration varies individually and between regions. The back is yellowish-brown in light voles, dark greyish-ochraceous in dark voles and fulvous-grey or buffy-grey in intermediate individuals. The fur is grizzled by black tips of hairs which are abundant in dark voles and sparse or absent in light animals; black hairs are scarcer on the sides of the neck and on the flanks which fade to clear fulvous. Underside is greyish-yellow or buffy-whitish. Hair bases are invariably dark ashy-grey. The tail is whitish to light cream-grey or buffy-brown; it is uniformly light in pale individuals to distinctly bi-coloured in dark voles. Paws are whitish; the ears are light-grey.

The skull is shallower than in *fuscus*; the rostrum is downturned to a lesser degree, the nasals are slightly larger, the incisive foramina is narrower and slit-like (wider and oval in *fuscus*), bullae are somewhat larger (smaller in *fuscus*), and zygomatic arches are more expanded (ZgW/CbL=0.62–69 vs 0.55–0.62 in *fuscus*). The mandible has a more robust and deeper body (visibly lower in *fuscus*), a shorter articular process (long in *fuscus*), heavier angular process (slender and sickle-shaped in *fuscus*) and a less prominent alveolar process. Adult Blyth's scrub voles possess a sagittal crest in the interorbital region (Figure 188); subadults have a groove between the temporal ridges before they merge into a crest. The groove expands anteriorly forming a circular concavity immediately behind the nasals (similar to *Alexandromys fortis*). Incisors are less proodont than in *fuscus*. M_1 has 3 closed triangles (T1–T3); T4 is confluent with T5 and AC (Figure 189a',b'). In contrast to *fuscus*, the glans penis is shorter in *leucurus* (length=4.4–4.5 mm vs. 4.8–5.0 mm in *fuscus*) and narrower (width=2.5–2.8 mm vs. 2.8–3.0 mm in *fuscus*), but the proximal baculum is longer (length=3.0–3.4 mm vs. 2.9–3.1 mm in *fuscus*). The lateral distal baculum is cartilaginous in *leucurus* and slightly ossified in *fuscus* (Liu et al. 2012b).

Variation and subspecies. Different authors recognised either 3 (e.g. Luo et al. 2000) or 5 subspecies

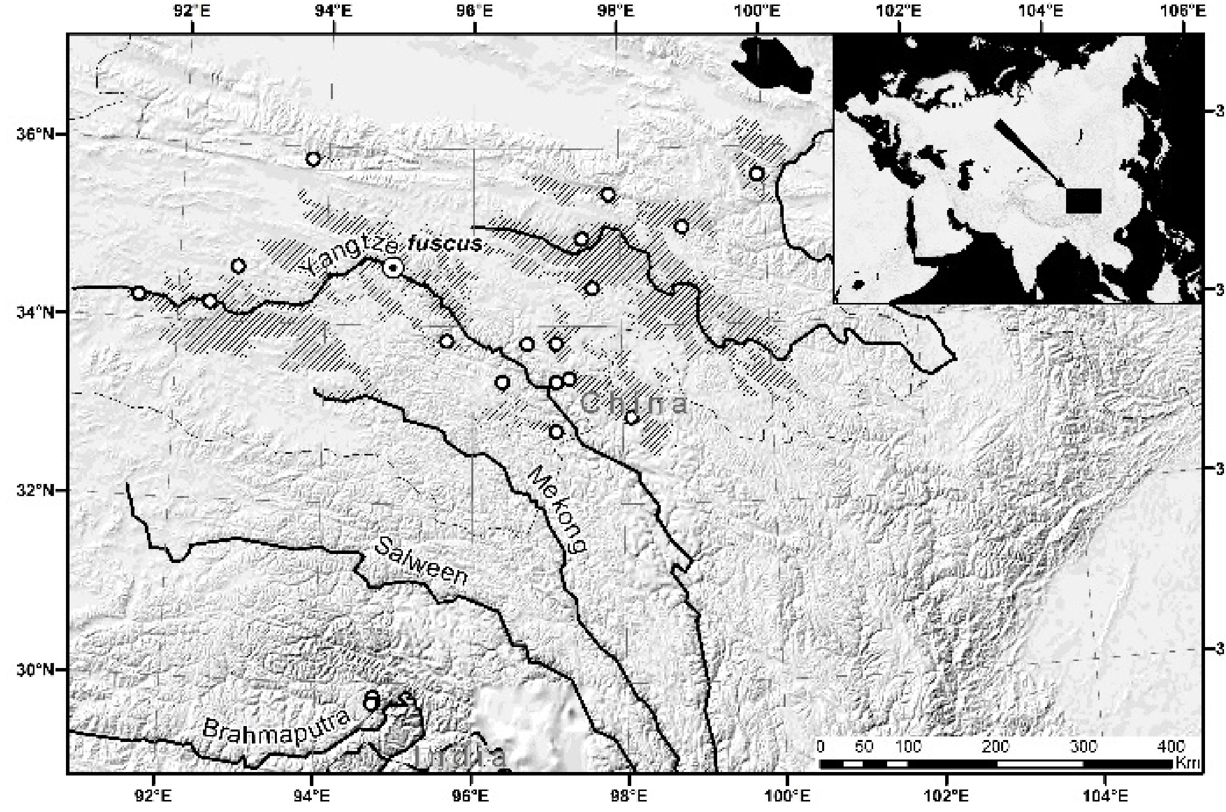


Figure 191: Distributional range of Büchner's scrub vole *Neodon fuscus*.

(e.g. Gromov & Polyakov 1977). In the past, Ellerman (1961) distinguished subspecies by the length of the bullae and colour. The size of bullae varies more than Ellerman had anticipated (cf. Mitchell & Derksen 1976) which left colour as the only trait used in subspecific taxonomy. Light coloured subspecies (the nominal, *everesti*, and possibly *tsaidamensis*) occupy the western, south-western, and north-eastern parts of the range; dark subspecies (*petulans* and *zadoensis*) occur sporadically along the eastern rim and are interspersed by populations of intermediate colour (classified as *waltoni* and *strauchi*). Variation in Blyth's scrub vole is an obvious mosaic of different colour types, combined with north-to-south cline in size. For this reason we do not classify populations to the subspecies level.

Neodon fuscus (Büchner 1889) – Büchner's Scrub Vole

Microtus strauchi var. *fuscus* Büchner 1889:125. Type locality subsequently restricted to the river "Zhi Qu, or Tongtian He" at ~"33°40'N, 96°15E"', China (Hoffmann 1996:164).

Taxonomy. In the past frequently classified in *Lasiopodomys*. Only rarely has *fuscus* been synonymised with *leucurus* (e.g. Ellerman 1941.)

Distribution (Figure 191). Endemic to China where confined to south-eastern Qinghai and very peripherally to Sichuan (known only from Shiqu; Liu et al. 2012b); a remotely isolated population was recently found in eastern Xizang (Mt. Sejila in Linzhi County; Wen et al., 2018). The distribution is estimated at 77,280 km². Habitat as in *leucurus*: humid to damp patches in high mountain (2,900–4,800 m a.s.l.) arid steppe and semi-desert; also lives on sandy substrate (Hoffmann 1996, Luo et al. 2000).

Characteristics. Dimensions: BWt=27–76 g, H&B=107–141 mm, TL=25–42 mm, HF=14–23 mm, EL=7.5–15 mm, CbL=27.2–31.3 mm, ZgW=15.0–18.5 mm, MxT=5.1–7.3 mm. Similar to *leucurus* but slightly larger with a relatively shorter tail (TL/H&B=0.18–0.28) and smaller ears. Dorsal fur is yellowish-brown to cloudy greyish-ochraceous; flanks are fulvous-cream to dull whitish and the belly is cream to whitish. Hair bases are slate throughout. Hairs of the auricular region are dirty-cream to buffy and contrast the darker and duller surrounding fur (Figure 192). The tail is fulvous with a brown terminal pencil in yellowish-brown voles and uniformly grey in dark animals. Ears are grey and the paws are buff. The skull is detailed under *leucurus*. Dentition: M_1 with 4 closed triangles, i.e., dental fields of T4–T5 alternate (Figure 189c-d). For glans penis and baculum, see under *leucurus*.

Variation and subspecies. Monotypic.

Figure 192: Taxidermic mount of *Neodon fuscus*; note the light patches in the auricular region. Voucher (Zoological Museum, St. Petersburg; ZIN 1908) was collected in 1884 at Odon Tala, Qinghai Province, China, during Przeval'skii's 4th expedition to Central Asia. Photo: B. Kryštufek.

Species group *irene*

Taxonomy. Sister position of *irene* with *linzhiensis* is evident from *Mt*-phylogenetic trees (Liu et al. 2017, Pradhan et al. 2019); *forresti* has not yet been sequenced.

Distribution. Eastern slopes of the Quinghai-Tibet plateau from Qinghai in the N, southward to eastern Xizang, Yunnan and northern Myanmar.

Characteristics. Small to medium-sized scrub voles with a rather short tail (TL/H&B≈0.35); there are 6 plantar pads and 8 nipples. M_1 is either pitymoid or with alternating triangles T4–T5; the AC usually lacks re-entrant angles LR5 and BR4. M^3 has 3–4 lingual and 3 labial salient angles.

Neodon irene (Thomas, 1911) – Chinese Scrub Vole

Taxonomy. *N. irene* was first regarded as a species in its own right but was relegated to a subspecies of *sikimensis* in the 1960s. Its previous rank was restored in Musser & Carleton (1993). Additionally, *forresti* was frequently misunderstood as a large form of *irene*; see under that species.

Distribution (Figure 193). Endemic to the eastern slopes of the Quinghai-Tibet plateau in southern Gansu, eastern Qinghai and western Sichuan; marginally present in eastern Xizang and northern Yunnan. The range is estimated at 352,110 km². Inhabits forest edges, meadows, shrubs and rocky habitats in cool temperatures and alpine zones (Lawrence 1982) at 1,435–4,500 m.

Characteristics. The smallest shrub vole with long ears projecting beyond the fur. The tail is short (TL/H&B=0.24–0.46), with a minute pencil (length≈1–1.5 mm). Fur is dense, soft and short (7–9 mm) with sparse protruding hairs measuring 9–11 mm. There are 6 nearly circular plantar pads which are of about equal size; metatarsal pads are placed one behind the other (Figure 183b). The dorsal fur is greyish-brown and grizzled due to scattered light hairs; flanks are lighter, greyer and slightly shaded buff; demarcation on the flanks is gradual. The belly is grey and frequently washed buffy; some hairs have white tips. Feet are pale brown, ears are grey; the tail is bi-coloured, dark brown above and whitish below. The skull is small and delicate with a long rostrum and narrow interorbital region. Temporal

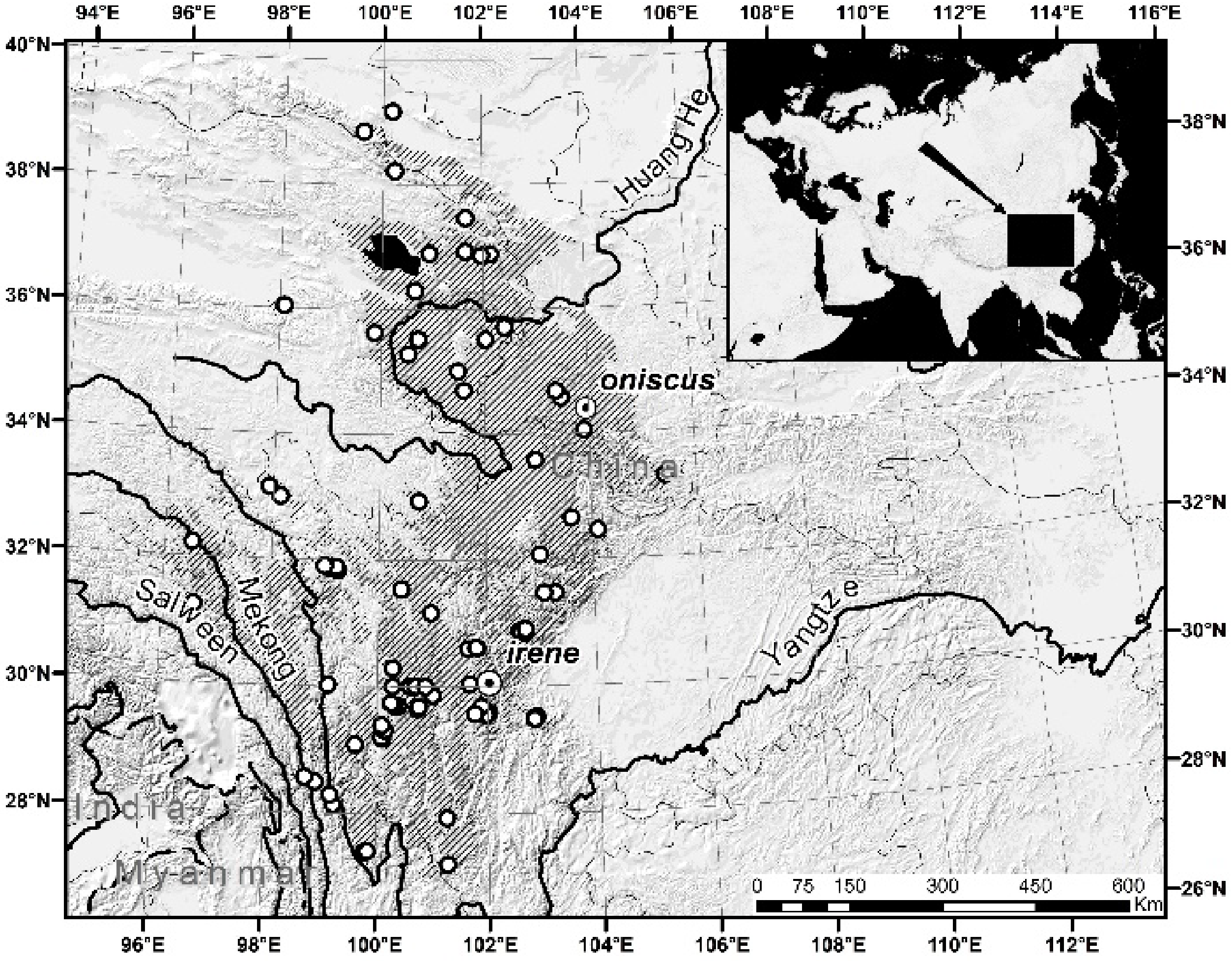


Figure 193: Distributional range of the Chinese scrub vole *Neodon irene*.

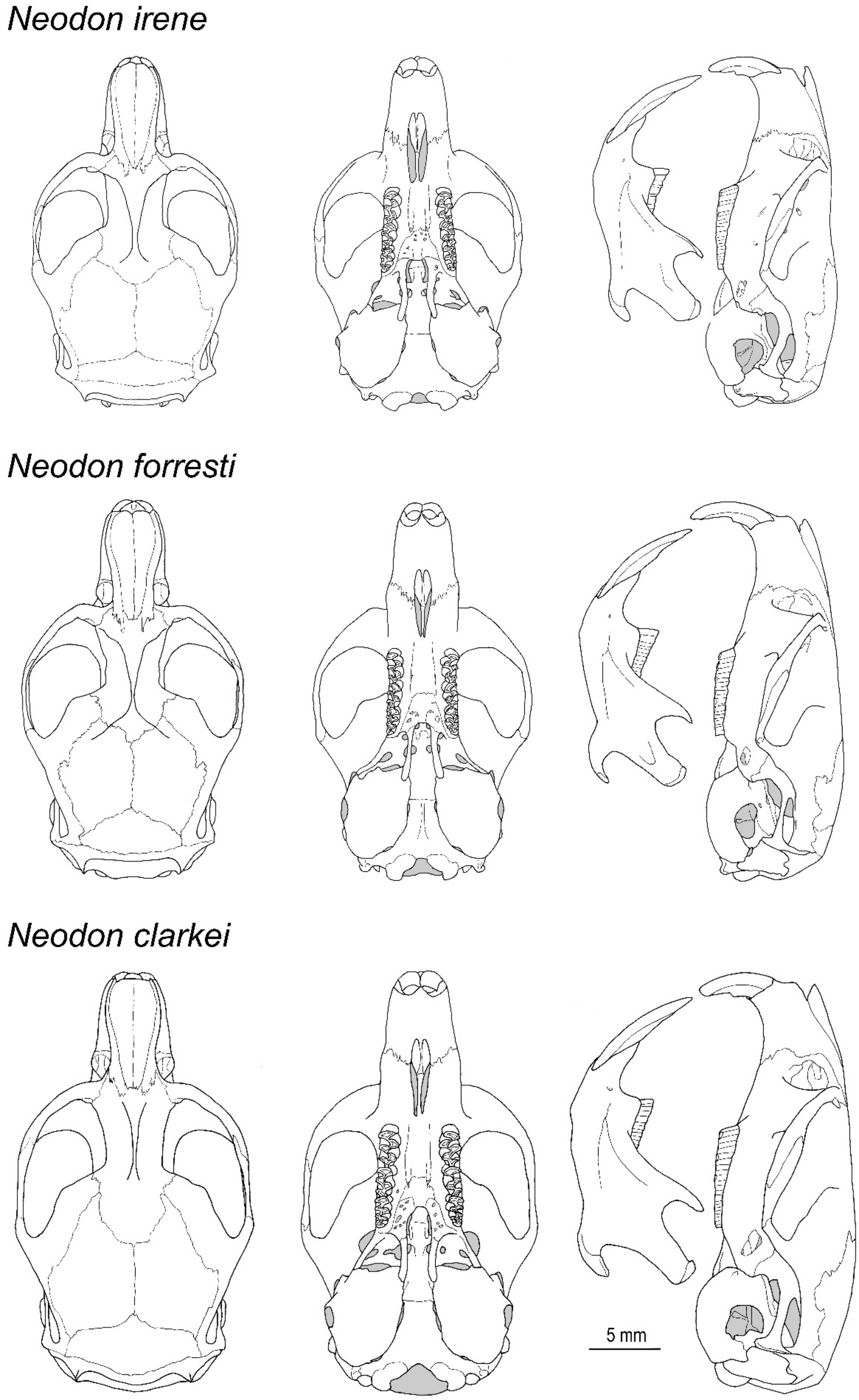


Figure 194: Skull in scrub voles from the *irene* and *clarkei* species groups (subgenus *Phaiomys;* top-to-bottom): *Neodon irene* (Kangding, western Sichuan, China; top), *N. forresti* (north-western Yunnan, China; middle), and *N. clarkei* (northern Myanmar; bottom).

ridges are restricted to the frontals and are swollen at their anterior end. Anteriorly, the ridges diverge and form a depression in-between (as in *leucurus*); posteriorly they merge to a sagittal crest. Incisive foramens are wide (Figure 194); bullae are small and filled with spongy bone for ~½ their volume (Allen 1940). Lateral pits on the posterior palate are moderately deep. Upper incisors are orthodont with indistinct longitudinal groove. About ½ of voles have 3 lingual salient angles on M^3 and the rest have 4 angles; there are invariably 3 salient angles on the outer side. M_1 has 5 salient angles on the lingual side and 3–4 prominent angles on the labial side; the antero-lingual angle BS4 is obtuse or absent. Triangles T4–T5 are usually confluent; AC is more or less isolated by deep re-entrant angles LR4 and BR3 (Figure 195a–c'). The proximal baculum is narrow with an abrupt basal expansion and triangular posterior profile; the bone is 2.80–3.00 mm long and 1.33–1.90 mm wide across the base. Central distal digit is robust and comparatively long (=1.17–1.33 m); the lateral digits are shorter (=0.58–0.80 mm), slender and not fully ossified (Liu et al. 2012b). Karyotype (2n=56, $NF_a=56$) consists of 1 small bi-armed and 26 acrocentric autosomal pairs, X is metacentric and Y is acrocentric (Sheftel et al. 2017).

Variation and subspecies. Allen (1940) recognised 2 subspecies (mapped in Luo et al. 2000), but expressed "extreme doubt" whether *oniscus* was worthy of taxonomic recognition; Wang (2003) regarded *irene* as monotypic. Using the *Cytb* gene, Fan et al. (2011b) screened the phylogeographic pattern between the upper stretches of the Yangtze (Jinsha) River and the Dadu River in western Sichuan. Despite only the nominal subspecies being surveyed, the resulting allopatric lineages were deeply divergent.

Neodon irene irene (Thomas, 1911)

Microtus irene Thomas 1911a:5. Type locality: "Ta-tsien-lu [Kangding], W. Sze-chuan [Sichuan]. 9000'–12,000' [2,745–3,660 m]" (as spelled in Thomas 1911d:173), China.

Distribution. Western Sichuan, north-eastern Tibet and north-western Yunnan.

Characteristics. Larger: BWt=19–39 g, H&B=80–112 mm, TL=20–48 mm, HF=16–19 mm, EL=13–15 mm, CbL=21.0–26.3 mm, ZgW=11.8–15.3 mm, MxT=4.9–6.2 mm. Molars tend towards complexity; M_1

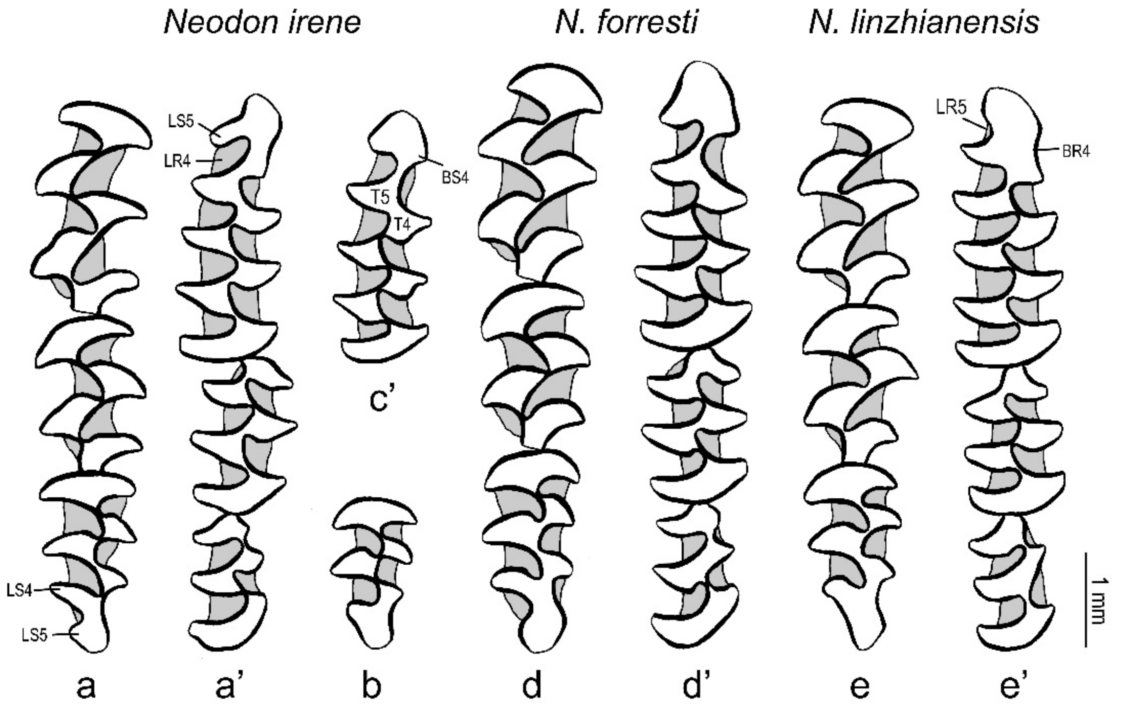


Figure 195: Molar pattern in voles from the *irene* species group (subgenus *Phaiomys*). *Neodon irene*: upper (a) and lower row (a'; Kangding, Sichuan, China); isolated M^3 (b) and M_1 (c'; Lianhuashan, Gansu, China). *N. forresti*: upper (d) and lower row (d'; north-western Yunnan, China). *N, linzhianensis*: upper (e) and lower row (e'; Xizang, China).

occasionally with shallow anterior re-entrant angles LR5 and BR4 on the AC; M^3 with 3–4 inner salient angles.

Neodon irene oniscus (Thomas, 1911)

Microtus oniscus Thomas, 1911f:723. Type locality: "40 miles [65 km] S.E. of Tao-chou, Kan-su [Gansu]. Alt[itude] 11,000' [3,350 m]", China.

Taxonomy. Described as a species and retained thus in Hinton (1923); Allen (1940) synonymised *oniscus* with *irene*.

Distribution. Eastern Qinghai and southern Gansu (central China).

Characteristics. Smaller: BWt=10–23 g, H&B=65–107 mm, TL=22–36 mm, HF=12–15.5 mm, EL=10–13 mm, CbL=21.8–22.6 mm, ZgW=12.5–13.2 mm, MxT=5.4–5.9 mm. Molars are less complex; M_1 with no re-entrant angles anterior to LR4 and BR3; M^3 with 3 inner salient angles.

Neodon forresti Hinton, 1923 – Forrest's Scrub Vole

Neodon forresti Hinton, 1923:156. Type locality: "upon the divide between the Mekong and Yangtze [Yángzǐ Jiāng] Rivers, N.W. Yunnan, in latitude 27° 30' N. Altitude 11,000' to 12,000' [3,350–3,660 m]" (p. 157), China.

Taxonomy. *N. forresti* was still treated as a species in its own right in Allen (1940), but afterwards was synonymised with *irene* (Ellerman 1947) or *sikimensis* (Gruber 1969); Musser & Carleton (2005) restored its specific rank, stressing that intergradation with *irene* was never demonstrated and that linear measurements do not overlap between these taxa. *N. forresti* is parapatric with *irene*.

Distribution (Figure 196). Known from merely 12 localities, 11 of which are in north-western Yunnan and a single one in northern Myanmar (Ellerman 1947). Occupies rocky habitats and alpine meadows at high

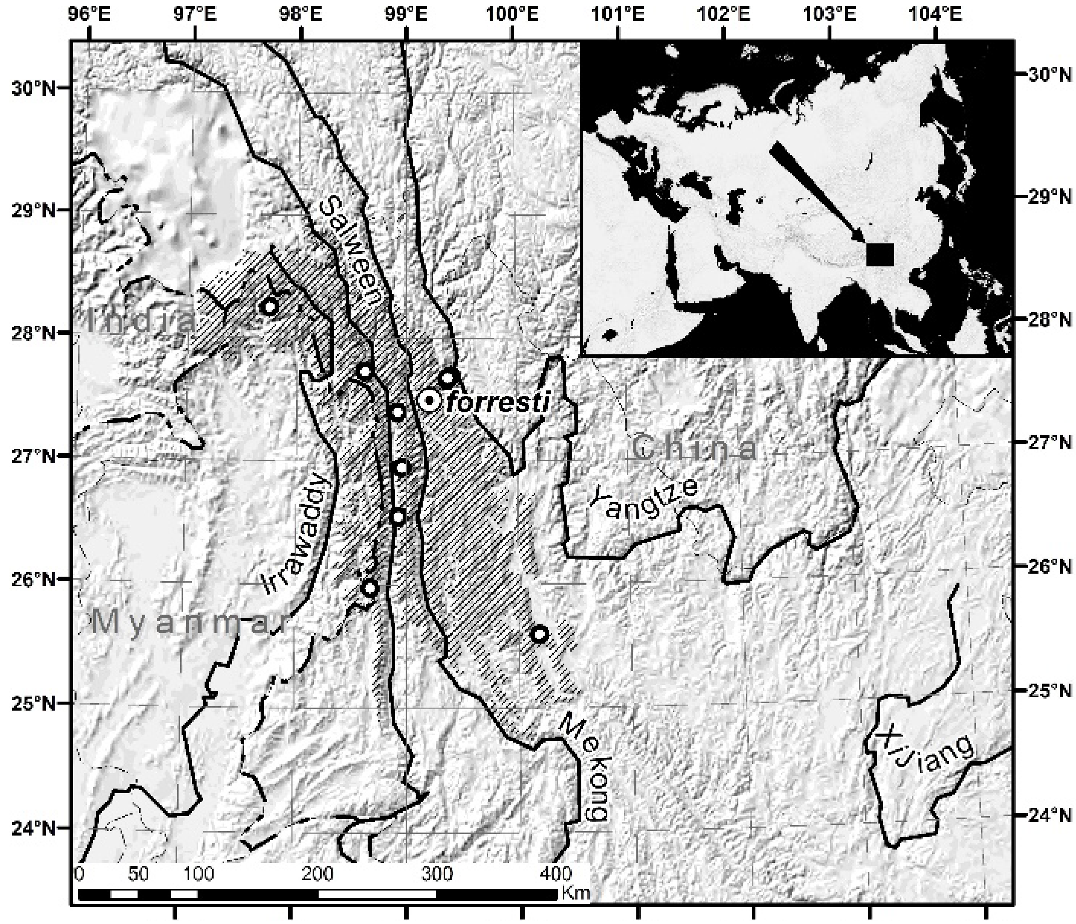


Figure 196: Distributional range of Forrest's scrub vole *Neodon forresti*.

altitudes (2,390–3,970 m). The entire range is estimated at 48,270 km².

Description. Similar to *irene* but larger: BWt=24–36 g, H&B=85–134 mm, TL=29–43 mm, HF=16–20 mm, EL=8–15 mm, CbL=24.9–28.5 mm, ZgW=14.1–17.0 mm, MxT=5.8–7.1 mm. Fur is soft, fine and long (up to 15 mm), dark brown above, slate and washed greyish-white below. Ears are blackish-brown, hardly longer than the surrounding hair; feet are greyish-white. Tail is distinctly bi-coloured, brownish to dusky above, dirty-white below. There are 5 palmar and 6 plantar pads. Skull is essentially as in *irene*, although larger and more ridged. Postorbital squamosal processes are prominent; temporal ridges are well-developed and form a sagittal crest in the interorbital region. Incisive foramina are in general shorter and bullae are larger than in *irene* (Figure 194) Molars as in *irene*; M^3 with 3–4 inner salient angles; M_1 without re-entrant angles anterior to LR4 and BR3 (Figure 195d).

Variation and subspecies. Monotypic.

Neodon linzhiensis Liu, Sun, Liu, Wang, Guo & Murphy, 2012 – Linzhi Scrub Vole

Neodon linzhiensis Liu, Sun, Liu, Wang, Guo & Murphy, 2012b:6. Type locality: "Gongbu Nature Reserve, eastern Linzhi, Xizang, China, 29.72891°N and 94.75630°E, 3890 m above sea level".

Distribution (Figure 197). Known from 5 localities in south-eastern Xizang Province, China, where captured on farmland. The range is estimated to cover ~6,000 km² at elevations of 3,415–4,540 m.

Description. Size between *irene* and *forresti*: BWt=26–48 g, H&B=92–115 mm, TL=24–39 mm, HF=16–20 mm, EL=12–15 mm, CbL=23.3–27.1 mm, ZgW=13.2–16.0

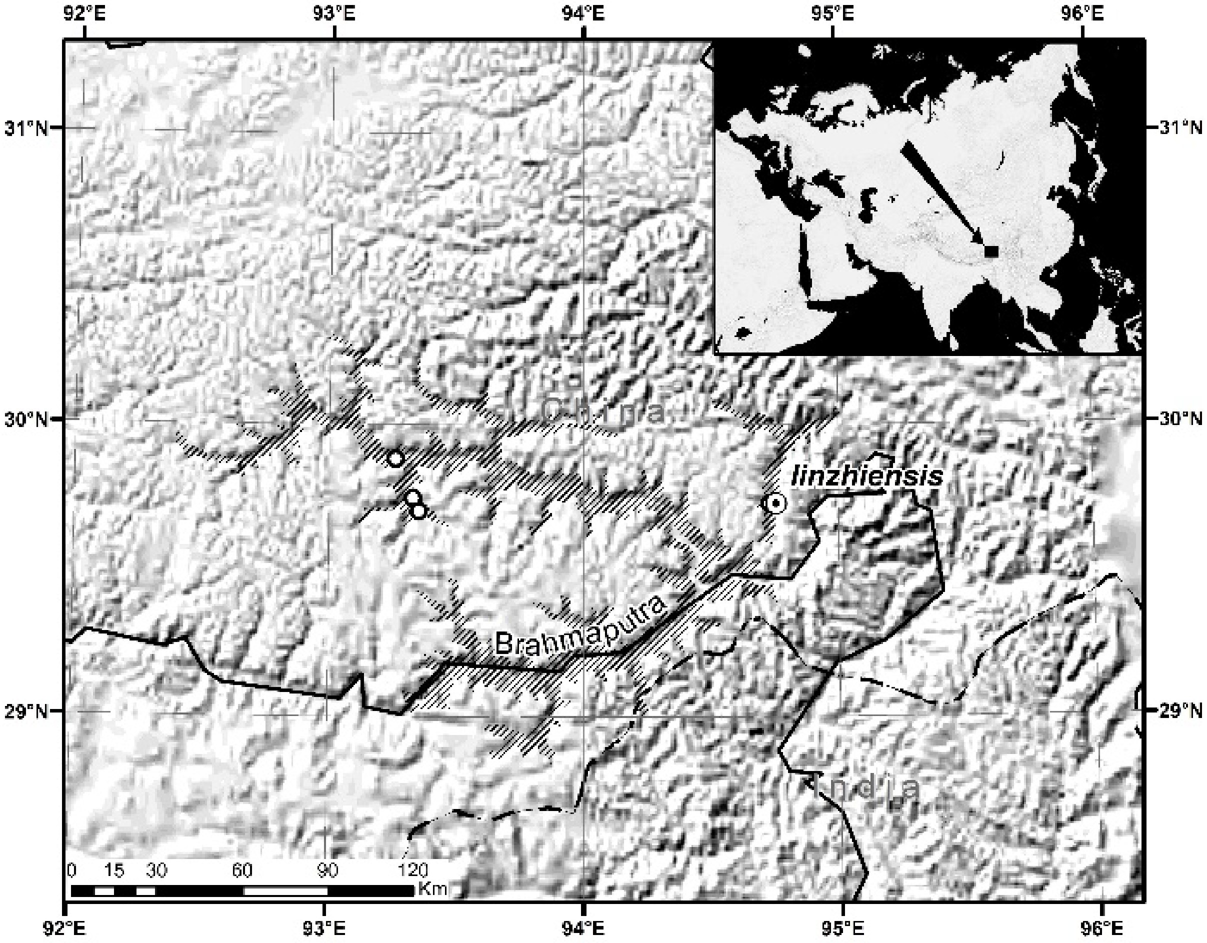


Figure 197: Distributional range of the Linzhi scrub vole *Neodon linzhiensis*.

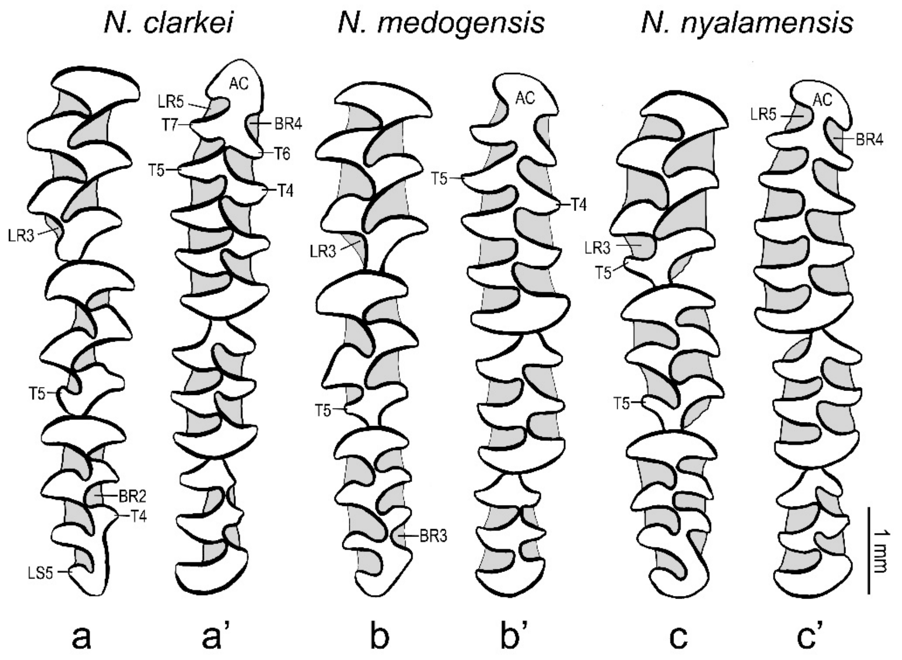


Figure 198: Molar pattern in voles from the *clarkei* species group (subgenus *Phaiomys*). *Neodon clarkei* : upper (a) and lower row (a'–Yunnan, China). *N. medogensis* : upper (b) and lower row (b'–Xizang, China). *N. nyalamensis* : upper (c) and lower row (c'–Xizang, China).

mm, MxT=5.3–6.1 mm (Liu et al. 2012b). Tail is relatively short (TL/H&B~0.33) and the ears only slightly overtop the fur. Hairs are rather long (length=8–10 mm), interspersed with scarce longer and stiffer hairs. Dorsal pelage is black-brown, the underside is lighter and slightly washed yellow; the transition on the flanks is gradual. Ears are the same colour as the dorsal fur; tail is bi-coloured, black-brown above and grey-white below with a short terminal pencil. Feet are dark grey; there are 5 palmar and 6 plantar pads. In adults the temporal ridges expand across the frontal, squamosal and parietal bones and form an interorbital crest. M^3 with 3 outer and 3–4 inner salient angles; M_1 with 6 inner and 4 outer salient angles and with alternating triangles T4–T5 (Figure 195e).

Variation and subspecies. Monotypic.

Species group *clarkei*

Taxonomy. Close relationships between *clarkei* and *medonensis* are evident from the concatenated *Cytb* and *COI* molecular trees. The phylogenetic position of *nyalamensis* is uncertain; it is either a sister species to *clarkei+medogensis*, or holds a basal position in *Phaiomys* (Liu et al. 2017).

Distribution. Mountains in southern Xizang, Yunnan and northern Myanmar, between the upper reaches of the Yangtze and Brahmaputra basins.

Characteristics. Long-tailed scrub voles with dark-brown to blackish fur. Glans penis is of average dimensions (length=3.80–4.50 mm, width=2.30–2.80 mm); baculum is a trident type. Females have 8 nipples. Molar pattern is similar to *N. sikimensis*. M^2 has an additional postero-lingual loop (T5) which opens to T4; M^3 is complex with 3 lingual and 2–3 buccal re-entrant angles. M_1 is complex with 5 lingual and 4 buccal re-entrant angles; triangles T4–T5 alternate; dental fields of T6–T7 are confluent and widely open into the AC which is either oval or arrow-shaped (Figure 198).

Neodon clarkei (Hinton, 1923) – Clarke's Scrub Vole

Microtus clarkei Hinton 1923:158. Type locality: "upon the divide between the Kiu-chiang [Jiujiang] and Salween Rivers in latitude 28° N. Altitude 11,000' [3,350 m]", Yunnan, China.

Taxonomy. Clarke's scrub vole was consistently classified in *Microtus* from its discovery in 1923.

Zagorodnyuk (1990) assigned *clarkei* to *Volemys* until molecular evidence demonstrated its close relationship with *Neodon* (Martínková & Moravec 2012). Hinton (1923) stressed the similarities between *clarkei* and *calamorum* (=*Alexandromys fortis*) and Ellerman (1941) classified *clarkei* in the *calamorum* group of *Microtus*. In a similar vein, Shenbrot & Krasnov (2005) assigned *clarkei* to *Alexandromys*.

Distribution (Figure 199). Range of 24,600 km² consists of 3 isolated parts: (i) in the Gaoligong and Gongshan Mts. (Yunnan, China) and between the Adung (Kachin State; Ellerman 1947) and Salween Rivers (Myanmar); (ii) mountains on both sides of the upper Yangtze River in Lijiang and Zhongdian Counties (northern Yunnan), and (iii) a small isolate in southern Yunnan (Mongtze in Gejiu County at the 23.322rd northern parallel). Clarke's scrub voles were captured in alpine meadows and coniferous forests at high altitudes (2,460–4,370 m).

A listing of Clark's scrub vole for south-eastern Xizang (Musser & Carleton 2005) was a misinterpretation of an earlier report of *millicens* (Feng et al. 1986) which actually represented *medogensis* (Liu et al. 2017).

Characteristics. A large scrub vole: BWt=32–47 g, H&B=107–134 mm, TL=55–67 mm, HF=19–23 mm, EL=12–17 mm, CbL=25.1–30.0 mm, ZgW=15.6–17.8 mm, MxT=6.5–7.9 mm. Tail is proportionally long (TL/H&B=0.48–0.58); there are 5 plantar pads; claws on front and hind limbs are of approximately the same size. The ears protrude above the fur which is soft, fine and fairly long (~12 mm). Dorsal pelage is dark brown and finely peppered with ochraceous or ferruginous hair tips, giving a bright brown effect. Underside is silver and lavishly clouded with slate hair bases; demarcation on flank is distinct but not sharp. The tail is dark brown above, grey below; paws are dirty white.

The skull is rather low with moderately expanded zygomatic arches (ZgW/CbL=0.58–0.63). In adult voles the supratemporal ridges approach closely in the central interorbital region but a narrow groove separates them even in adult individuals; therefore, there is no proper interorbital crest. At their anterior end the

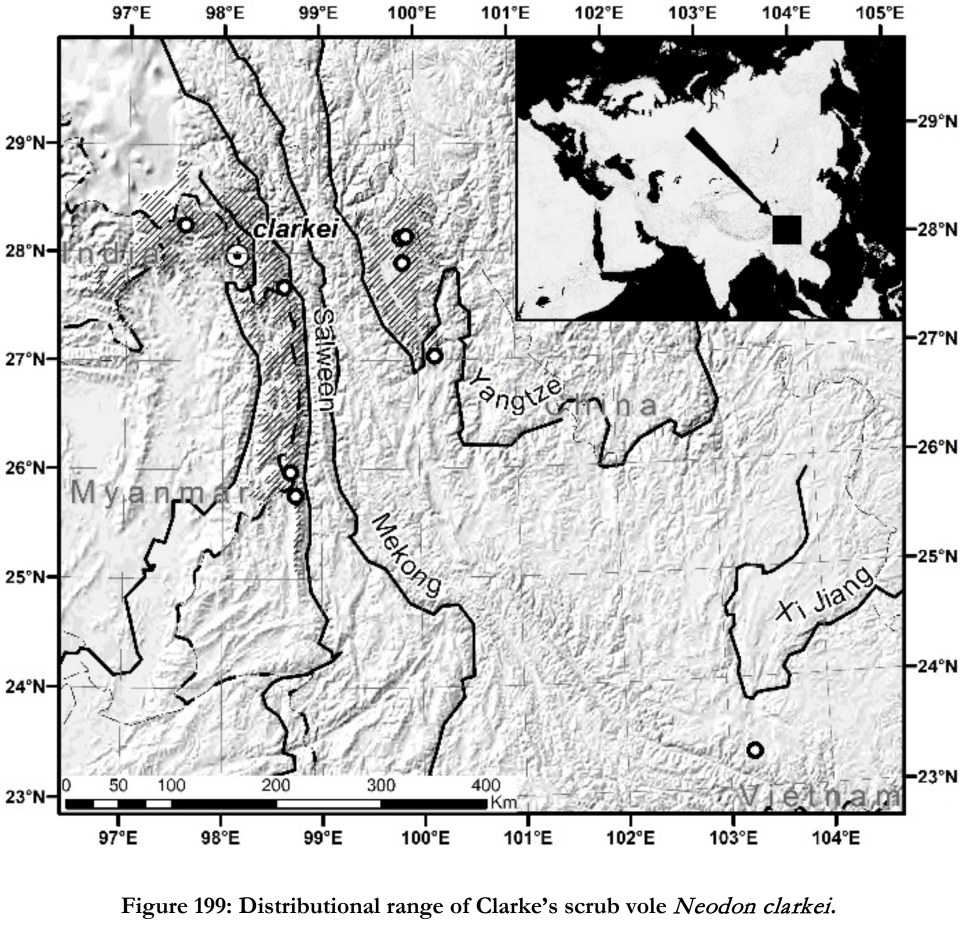


Figure 199: Distributional range of Clarke's scrub vole *Neodon clarkei*.

diverging temporal ridges swell and form a depression in-between (compare *Alexandromys fortis*). The sphaenoidal angle of the parietal is usually prolonged and nearly reaches the level of the blunt postorbital processes of the squamosal. The anterior edge of masseteric plate is concave. When viewed from above, the anterior margin of the infraorbital foramen is gently notched. The nasal bone is bottle-shaped; the interparietal is large. Incisive foramina are long with convex lateral margins. Post-palatal pits are of normal size but shallow and the crest between them is low. Bullae are rather small. Mandible shows no peculiarities and the alveolar bulge is blunt. Incisors are orthodont (Figure 194). The M^1 has 4 alternating triangles behind the anterior prism. The supplementary triangle T5 on the M^2 is vestigial and widely opens into the dental field of T4. The postero-buccal re-entrant angle on the M^3 is feeble and there is no true salient angle on the buccal side behind T4. Lingual salient angles LS4–LS5 and the outer triangle T4 are incorporated into the posterior cap. M_1 has 2 sets of triangles (T4–T5 and T6–T7) which are mutually isolated by deep re-entrant angles LR4–BR3; T4–T5 alternate but T6–T7 are confluent and open into AC. The anteriormost re-entrant angles LR5 and BR4 are moderately deep; the latter angle in particular is frequently shallow (Figure 198a). The proximal baculum (length=2.8 mm) has a very short basal expansion (width=1.5 mm). Distal baculum remains cartilaginous; length is 1.0 mm (central digit) and 0.7 mm (lateral digits).

Variation and subspecies. Monotypic.

Neodon medogensis Liu, Jin, Liu, Murphy, Lv, Hao, Liao, Sun, Tang, Chen & Fu, 2017 – Medog Scrub Vole

Neodon medogensis Liu, Jin, Liu, Murphy, Lv, Hao, Liao, Sun, Tang, Chen & Fu, 2017:178. Type locality: "Mêdog (Motuo) county; 29.73815°N, 95.67496°E; 3,410 m a.s.l.", Xizang (Tibet), China.

Taxonomy. The first vouchers of *medogensis*, collected in the 1980s, were classified as a "Zayü form" (from southern Zayu, Xizang) of *Volemys millicens* (Wang 2003; see also comments on *clarkei*).

Distribution (Figure 200). Known from 2 localities in Nyalam (Nielamu) County (southern Xizang, China) on the left bank of Koshi (Pochu) River (Brahmaputra River Basin). Voles were collected inside a bamboo

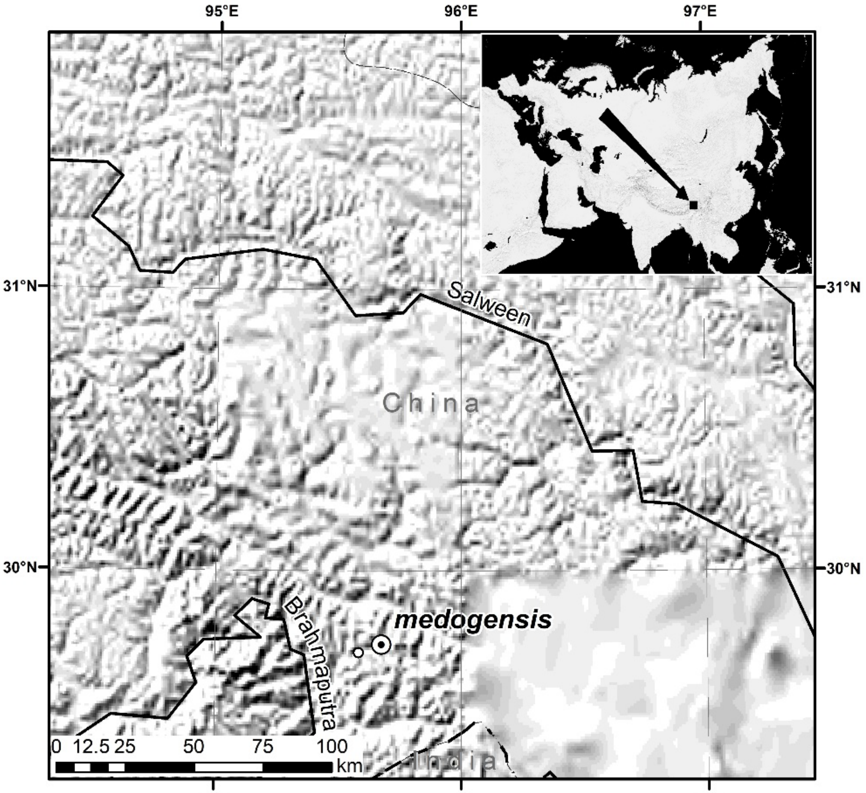


Figure 200: Distributional range of the Medog scrub vole *Neodon medogensis*.

stand and in a spruce forest; the humus layer was thick in both habitats. The elevation was 2,770 m and 3,410 m, respectively (Liu et al. 2017).

Characteristics. Moderately large scrub vole: BWt=26–41 g, H&B=89–110 mm, TL=43–55 mm, HF=18–20 mm, EL=12–15 mm, CbL=24.0–28.1 mm, ZgW=13.4–16.6 mm, MxT=6.0–7.1 mm (Liu et al. 2017). Tail is comparatively long (TL/H&B=0.42–0.55); there are five palmar and 6 plantar pads. Ears are densely clad with grey hairs and slightly overtop the pelage. Fur is soft and long (~10 mm) with scarce protruding hairs. Dorsal side is blackish-brown and clearly demarcated from the light-grey underside; hair bases are slate. Tail is faintly bi-coloured, blackish-grey above, light grey below; terminal pencil is short and paws are grey. Skull shows no peculiarities; zygomatic arches are moderately expanded (ZgW/CbL≈0.60) and the dorsal profile is evenly convex. Temporal ridges merge in the interorbital region to form a sagittal crest. The nasals are wider anteriorly than behind; incisive foramina are short. Dental pattern is like in *clarkei* (Figure 198b); in more than ½ of individuals, the M^3 has 3 re-entrant angles on the outer side (Liu et al. 2017). The proximal baculum is comparatively short (2.45–2.50 mm) with compressed basal expansion (width=1.40–1.60 mm); length of distal baculum is 0.90–1.10 mm (central digit) and 0.42–1.10 mm (lateral digit); lateral digits are ossified.

Variation and subspecies. Monotypic.

Neodon nyalamensis Liu, Jin, Liu, Murphy, Lv, Hao, Liao, Sun, Tang, Chen & Fu, 2017 – Nyalam Scrub Vole

Neodon nyalamensis Liu, Jin, Liu, Murphy, Lv, Hao, Liao, Sun, Tang, Chen & Fu, 2017:179. Type locality: "Nyalam (Nielamu) county; 28.08152°N, 85.99854°E; 3200 m a.s.l.", Xizang", China.

Distribution (Figure 201). Known from 2 localities in Nyalam (Nielamu) County (southern Xizang, China) on the right bank of the Yarlung Tsangpo River. Vouchers were captured in a bamboo scrub and in a sparse spruce forest with dense bamboo undergrowth. Substrate was sandy with boulders. The altitude was 3,255 and 3,650 m a.s.l., respectively (Liu et al. 2017).

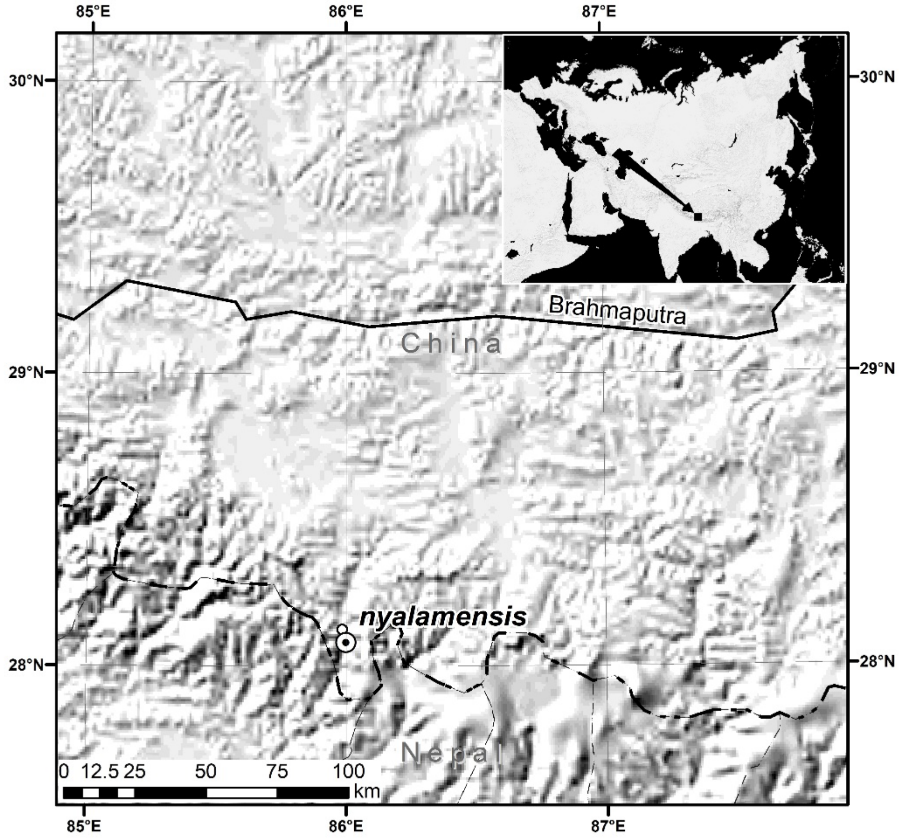


Figure 201: Distributional range of the Nyalam scrub vole *Neodon nyalamensis*.

Characteristics. A moderately large scrub vole: BWt=26–36 g, H&B=98–115 mm, TL=39–50 mm, HF=17–20 mm, EL=11–13 mm, CbL=24.1–27.1 mm, ZgW=14.0–15.7 mm, MxT=6.2–6.5 mm (Liu et al. 2017). The tail is proportionally shorter than in *clarkei* and *medogensis* (TL/H&B=0.37–0.44). Ears are nearly bare and only slightly overtop the hairs. There are 5 palmar and 6 plantar pads. Fur is fine, long (8–10 mm) and without protruding hairs. Dorsal pelage is grey with a buffy shade; underside is dark grey and the transition on the flanks is gradual. The tail is grey, more blackish above and lighter below; the terminal pencil is feeble. Paws are blackish-grey. The skull is of average proportions (ZgW/CbL≈0.59) and the dorsal profile is evenly bent. The interorbital region has a sagittal crest; postorbital processes of the squamosal are more prominent than in *clarkei* or *medogensis*. Incisive foramina are long; bullae are small. Incisors are orthodont. The M^1 has a deep postero-lingual re-entrant angle LR3 and an additional salient angle T5; there are 4 salient angles on the inner side. M^2–M^3 as in *clarkei*; M_1 as in *medogensis*, except that T4–T5 are confluent and the re-entrant angles LR5 and BR4 are deeper. The proximal baculum is the longest in the species group: length×width across basal expansion=2.90–3.15×1.40–1.80 mm; the central distal baculum (length=1.60–1.70 mm) averages >50% of the length of proximal baculum (corresponding values in *clarkei* and *medogensis* are 25% and 27%, respectively). Lateral digits (length=0.35–0.75 mm) are faintly ossified (Liu et al. 2017).

Variation and subspecies. Monotypic.

GENUS: *Alexandromys* Ognev, 1914 – Grass Voles

Taxonomy. *Alexandromys* was established more than a century ago but repudiated by Vinogradov & Obolensky (1927) and sank into oblivion in the decades to follow. Allen's (1940) suggestion that *Alexandromys* might be synonymous with the Nearctic *Aulacomys* Rhoads, 1894, did not attract much attention. For most of the 20th century, grass voles were classified in *Microtus* and were occasionally lined up into several species groups which also included voles now in *Microtus, Iberomys* (Gromov & Polyakov 1977), and *Neodon* (Musser & Carleton 2005). Alternatively, grass voles were classified in 3–4 subgeneric groups (*Alexandromys, Arvalomys, Lasiopodomys*, *Microtus, Pallasiinus*, *Stenocranius, Sumeriomys, Suranomys* and *Volemys*) with not much congruence among different authors.

A novel look at the taxonomic position of grass voles was prompted by karyology. Namely, several species (*oeconomus, fortis, kikuchii*, and *montebelli*) were shown to have synaptic sex chromosomes capable of pairing in male meiosis (for reviews see Borodin et al. 1995, Levenkova et al. 1997, Mekada et al. 2001); in the majority of *Microtu*s s.lat. the heterosomes are asynaptic. Subsequent phylogenetic reconstructions using nucleotide sequences provided evidence regarding the monophylly of *Alexandroyms* (Bannikova et al. 2010, Haring et al. 2015, Steppan & Schenk 2017). *Alexandromys* differs from *Microtus* s. str. and *Terricola* in the peculiarities of its reproductive behaviour (Zorenko 2007), including acoustic communication (Rutovskaya 2020). *Alexandromys* started entering general use in the 1990s, firstly as a subgenus.

Divergence between *Microtus* and *Alexandromys* putatively dates back to the Pliocene-Pleistocene border (2.42 Mya) while basal radiation in *Alexandromys* occured at 1.19 Mya (Bannikova et al. 2010) or 1.94 Mya (Thanou et al. 2020). There is little consensus regarding further divergences within the genus. Based primarily on a phylogenetic tree in Steppan & Schenk (2017) we recognise 3 subgenera, *Alexandromys* (with 3 species groups), *Oecomicrotus*, and *Yushanomys* sgen. n. One species is left unassigned to a subgenus.

Distribution. A Holartic genus, but the majority of species is restricted to Asia east of Baikal and Tibet. In the north grass voles go beyond the Arctic Circle and in the south they reach the Pearl (Zhuijang) River (southern China) and Taiwan, both deeply inside the Palaearctic-Oriental transitional zone.

Description. (Figure 202). Body robust with a short, thick neck and a large, wide and blunt head. Tail is long (TL/H&B≈0.35–0.65); the annulation is frequently not concealed and the terminal pencil is weak. The ears scarcely appear above the fur; the tragus is low and the antitragus is high. Eyes are small and the nostril pad is inconspicuous. Front thumb is large, usually with a nail and rarely bearing a claw (in *mongolicus*); the remaining front claws are robust and exceptionally slender (Figure 203). There are 5 palmar and 5–6 plantar pads with considerable individual variation (Figure 204). An asymmetric number of plantar pads was scored in 3.3% of *A. mujanensis* and 13.4% of *A. sachalinensis* (Meyer et al. 1996). The spaces between the pads are minutely tubercular and the area behind them is densely hairy. Fur is rather long and shaggy. Individual hairs are dark throughout or banded subterminally with ochraceous-buff, frequently producing a grizzled appearance. There are 8 nipples but the pectoral pair is absent in *kikuchii*. Flank glands are located on the hips. Skull is large and

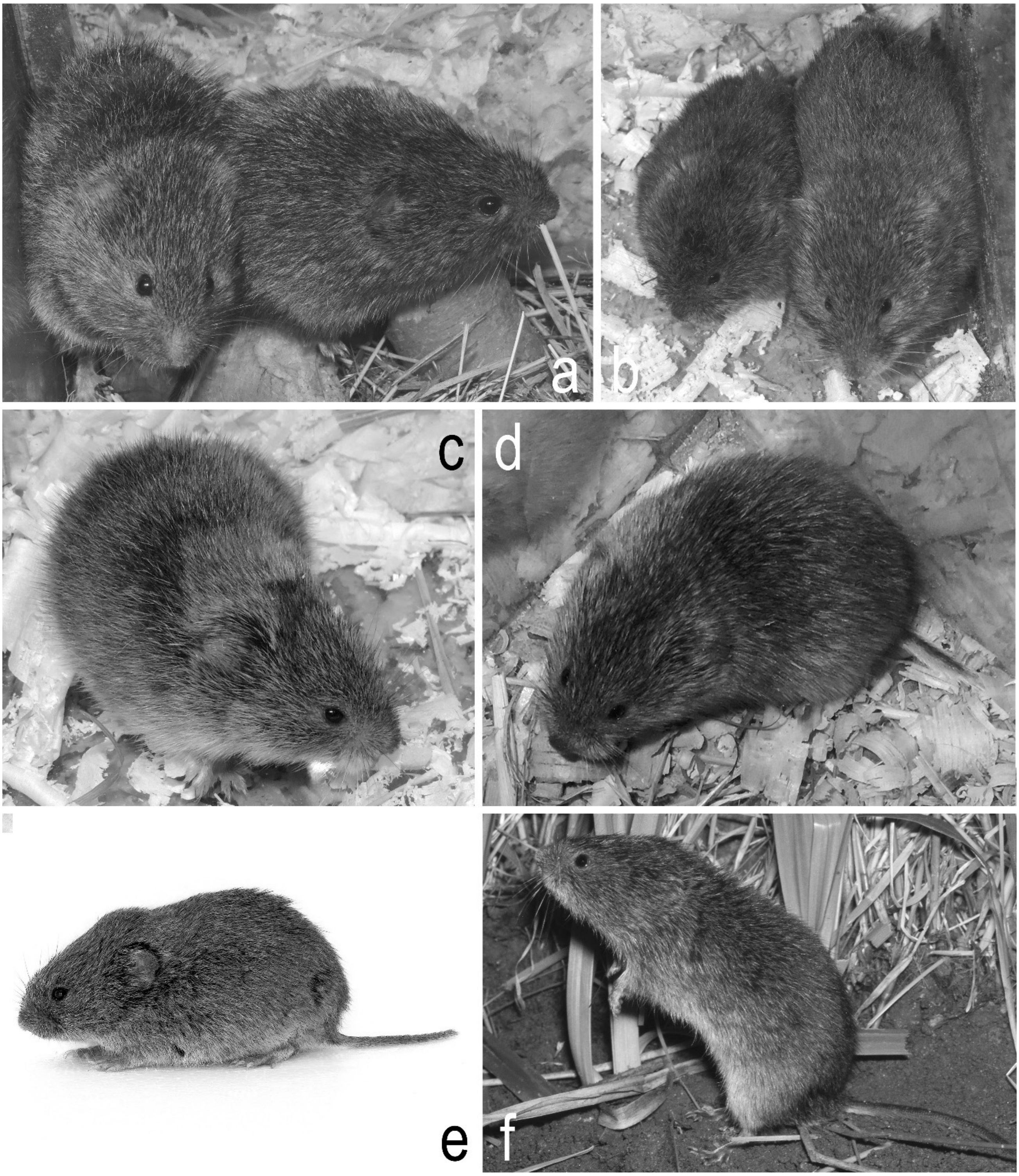


Figure 202: Grass voles (*Alexandromys*): a–*A. mujanensis*; b–*A. shantaricus gromovi*; c–*A. middendorffii*; d–*A. mongolicus*; e–*A. montebelli*; f–*A. oeconomus*. Photo courtesy: Masahiro A. Iwasa (e), Miloš Anděra (f), B. Kryštufek (a–d).

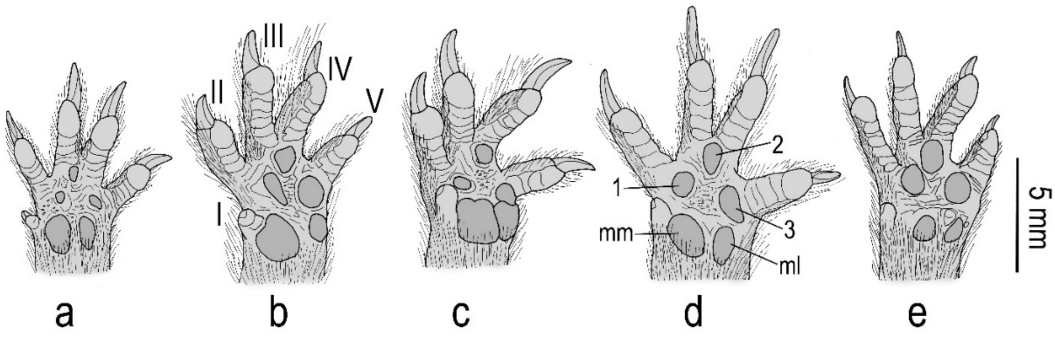


Figure 203: Left palm in grass voles *Alexandromys*: a–*A. alpinus* (Khangai, Mongolia), b–*A. oeconomus* (Kuantun, China), c–*A. limnophilus* (Kuh-Moryu on the Dzad-Han River, Mongolia), d–*A. montebelli*, e–*A. kikuchii*.

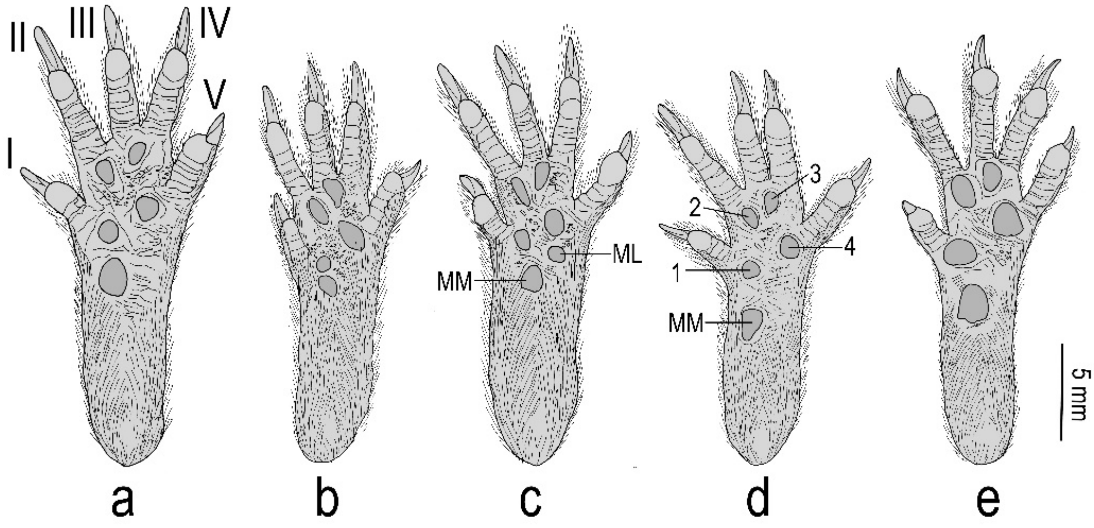


Figure 204: Left sole in grass voles *Alexandromys*: a–*A. fortis* (Primorsky Krai, Russia), b–*A. maximowiczii* (Transbaikal Russia), c–*A. oeconomus* (Lappland, Norway), d–*A. montebelli*, e– *A. kikuchii*.

deep; zygomatic arches are strong and massive but not greatly expanded, braincase long and narrow. Supratemporal ridges are frequently weak but merge into the sagittal crest which often starts in the posterior part of the interorbital constriction. Molars do not differ appreciably from *Microtus*; M_1 has 4 closed alternating triangles; T5 is usually closed. The anteroconid complex displays high intraspecific heterogeneity which blurs the differences between species (Pozdnyakov 1996, Voyta et al. 2019). Baculum is of trident type, nonetheless the distal digits are not uncommonly small or even dwarfed. Karyotype: 2n=30–52; sex chromosomes are synaptic and do not form a synaptonemal complex (X-Y pairing) at pachytene. The karyotype is polymorphic in several species.

Key to species

1a) Triangle T5 on M_1 usually opens into AC; plantar pads typically 6 ...…......…………....……….…..........… 2

1b) Triangle T5 on M_1 usually closed; plantar pads usually 5 (6 in *shantaricus*) …………………...…......... 3

2a) The angle at which the nasals slope downward (in the lateral view) is acute; M^3 with confluent dental fields of T4 and the posterior cap; 2n=38 ………. *limnophilus*

2b) The angle at which the nasals slope downward (in lateral view) less acute; M^3 with closed T4; 2n=30 ……………………………………….…….. *oeconomus*

3a) Females with 2 pairs of nipples (both inguinal); plantar pads large; front claws short and weak; endemic to Taiwan …………………………..……..… *kikuchii*

3b) Females with 4 pairs of nipples; plantar pads small; front claws long and usually robust; absent from Taiwan …………………………………………................. 4

4a) Pelage lacks long protruding hairs; 2n=30; endemic to Japan …….. *montebelli*

4b) Pelage with sparse long protruding hairs; 2n>30; occur on mainland Asia and Sakhalin …….................... 5

5a) Sperm head falciform; supratemporal ridges do not merge into sagittal crest; the anterior frontals with a

distinct depression behind the nasals and between the diverging supratemporal ridges ……………………… *fortis*
5b) Sperm head oval; supratemporal ridges frequently merge into sagittal crest; the anterior frontals behind the nasals and between the diverging supratemporal ridges are usually flat ……………………………………… 6
6a) Medial distal baculum long (~½ the proximal baculum); size large; endemic to Sakhalin ……………………………………………… ...*sachalinensis*
6b) Medial distal baculum shorter than ½ the proximal baculum; present on mainland Asia ………………………... 7
7a) Plantar pads usually 5; snout brown ………………….. 8
7b) Plantar pads 6; snout brightly buff ……… *shantaricus*
8a) Tail short (TL/H&B usually <0.30), densely hairy (underlying annulation concealed), sharply bi-coloured …………………………………………………………………… 9
8b) Tail long (TL/H&B usually >0.30), thinly to densely hairy (annulation frequently exposed), uniformly dark or faintly bi-coloured ………………………………………… 10
9a) Larger: HF≥15.2 mm, CbL≥24.5 mm; pencil at the tail tip >10 mm; triangle T6 on M^3 present and prominent (4 outer salient angles) ………. *middendorffii*
9b) Smaller: HF≤16.5 mm, CbL≤26.5 mm; pencil at the tail tip <9 mm; triangle T6 on M^3 vestigial or absent (3 outer salient angles) …………………………………… *alpinus*
10a) Size smaller; X chromosome is acrocentric ……………………………………………………… *maximowiczii*
10b) Size larger; X chromosome is submetacentric ……………………………………………………………………………11
11a) Diploid number of chromosomes 2n=46–49; present in the area of Lake Baikal (west of 120th meridian) ……………………………………………. *mujanensis*
11b) Diploid number of chromosomes 2n=36–40; present in the Khabarovsk and Amur districts (east of the 120th meridian) ……………………………. *evoronensis*

SUBGENUS: *Alexandromys* Ognev, 1914

Alexandromys Ognev, 1914:109. Type species by monotypy: *Microtus pelliceus* Thomas (=*fortis* Büchner).

Taxonomy. Traditionally encompassed grass voles with 5 plantar pads and a closed triangle T5 on M_1, i.e. all species except *oeconomus* and *limnophilus*. In the present definition, the subgenus contains 3 species groups (*fortis, maximowiczii* and *mongolicus*).

Distribution. Asiatic, with a single species marginally present in north-eastern Europe.

Characteristics. Morphologically diverse assemblage of unspecified synapomorphies. Characteristics variable; plantar pads usually 5; 8 nipples; triangle T5 on M_1 isolated.

Species group *fortis*

Alexandromys fortis (Büchner, 1889) – Reed Vole

Taxonomy. The earliest reports were most likely by Schrenck (1859) as *Arvicola amphibius* (cf. Sowerby 1923, Vinogradov & Obolensky 1927) and *Arvicola saxatilis* (nomen dubium). Subsequently, the reed vole has been recounted as *calamorum* (Hinton 1923), *michnoi* (Vinogradov 1933) or *pelliceus* (Sowerby 1923, Kuroda 1938, 1939). Some authors split *fortis* into 3 (Meyer et al. 1996) or 4 species (Vinogradov & Obolensky 1927): *fortis, calamorum, pelliceus* and *michnoi*. Current taxonomic scope was defined in Allen (1940) and Ognev (1950). Several authors (Heptner & Shvetsov 1960, Zimmermann 1964) synonymised *fortis* with *maximowiczii*.

The nearest relative to *fortis* is not known with certainty and different markers have not provided conclusive results. The putative sister species to *fortis* depends on the marker used: *gromovi* (=*shantaricus*; allozymies; Frisman et al. 2009), *limnophilus* (*Cytb;* Bannikova et al. 2010), or *sachalinensis* (nuclear sequences; Lissovsky et al. 2018a). In the results from Steppan & Schenk (2017), *fortis* holds a sister position to the *maximowiczii* and *mongolicus* species groups.

Distribution (Figure 205). Range of the reed vole (area=1,712,000 km^2) covers eastern Asia to the east of Baikal Lake, northern Mongolia, Inner Mongolia and Sichuan (at ~101st–102nd meridian) and between the line that connects–Sakhalin in the north and the Pearl (Zhuijang) River in the south. This vole ranges from mesic intrazonal habitats in deserts to boreal coniferous forests. It closely associates with lush and dense riparian vegetation surrounding aquatic habitats from sea level to 2,515 m a.s.l., i.e. river valleys, banks of streams, reeds, marshy meadows, and flooded plains. Occupies more dump sites where sympatric with *maximowiczii* (Dymin 1974). Its range is fragmented at various spatial scales with major patches in (i) Buryatiya (Russia) and adjacent parts of northern Mongolia, (ii) Zabaykalskiy Krai (east of Lake Baikal, Russia), north-eastern Mongolia, the upper reaches of the Amur and adjacent northern parts of Nei Mongol (China), (iii) the middle reaches of Amur, along Zeya and Ussuri Rivers (Russia), in Heilongjiang, Jilin Liaoning (China), and Korea (as far south as Jeonranamdo on the islands of Dadohaesang National Marine Park), (iv) along the north-western coast of the Sea of Japan on the eastern slopes of the Sikhote-Alin Range (Khabarovskiy and Primorskiy Krai, Russia); (v) several fragments at and around the great bend of the Huang He River in southern parts of Nei Mongol, Ningxia, Shaanxi and western Gansu, and (vi) between the Yangtze and Zhuijang Rivers. Further smaller isolates (e.g. Nikolayevsk-na-Amure) are scattered throughout the range. The reed vole is also present on northern Sakhalin, the nearby Chaichiy Island, and on 19 islands located in the Sea of Japan off the coast of the Primorye region, Russia (north-to-south): Skrebtsova, Russkii, Popova, Naumova, Malyi, Klykova, Reineke, Rikord, Putyatin, Karamzina, Sibiryakova, Lisiy, De-Livrona, Gil'debrandta, Durnovo, Matveevo, Bol'shoi Pelis, Vera, and Antipenko (Sheremetyev 2004).

Characteristics. A large grass vole externally resembling the aquatic *Arvicola* but the hind foot is decidedly shorter (HfL≤27 mm), less robust and with more delicate claws. The tail is relatively long

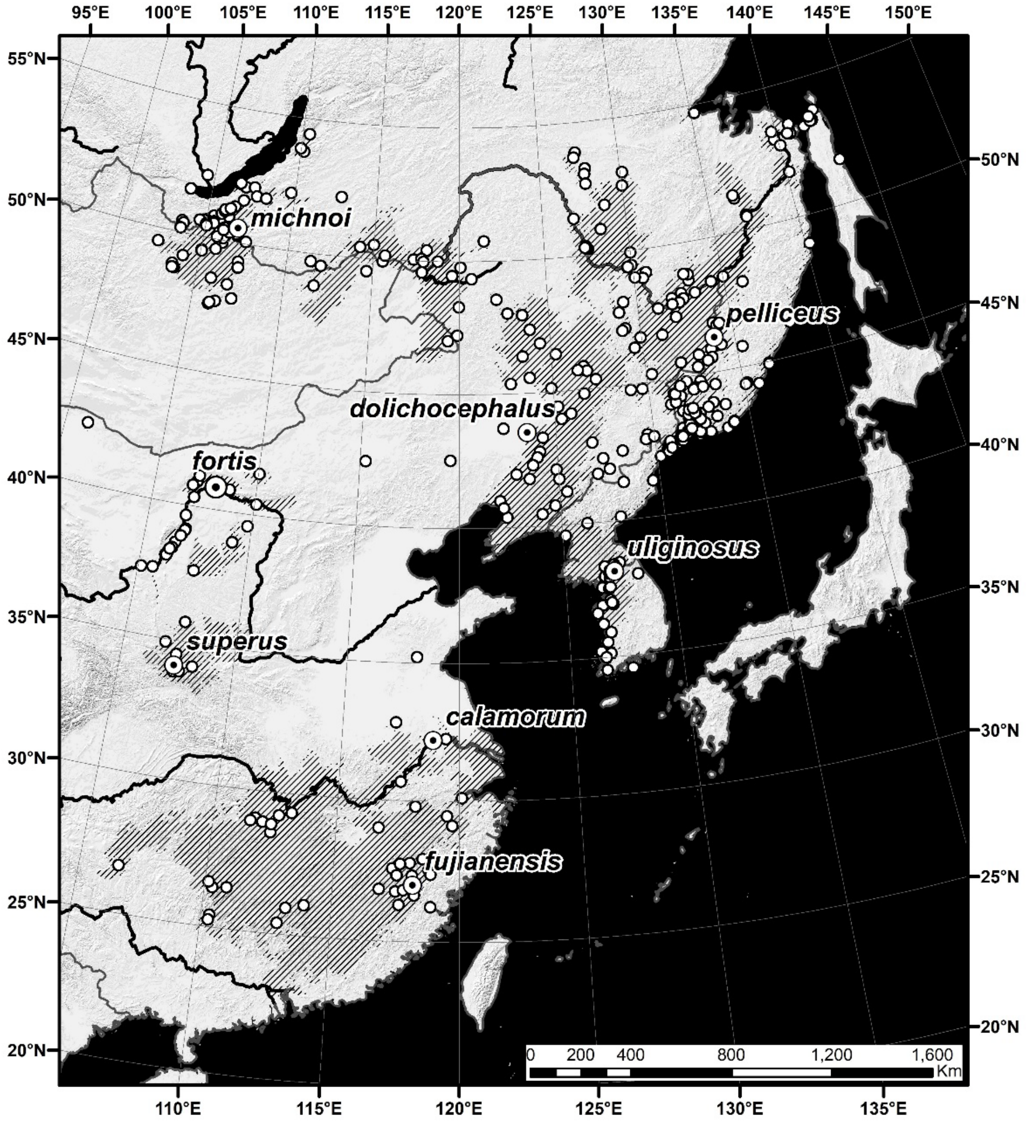


Figure 205: Distributional range of the Reed vole *Alexandromys fortis*.

(TL/H&B=0.31–0.56) and densely clad with hair; terminal pencil is long (6–10 mm). There are 5 plantar pads (Figure 204a); the 6th rudimentary pad is present in 13.5% of voles (Meyer et al. 1996). Fur is soft, 8–12 mm long on the midback, with sparse longer hairs measuring 12.5–17 mm. Dorsal pelage is bright-tawny or cinnamon brown to dark brown, frequently glossy and grizzled by buffy hair tips; cheeks, inner surface of ears and flanks are occasionally washed fulvous. Underside is whitish or grey, clouded by slate underhair and in some populations tinted buffy; demarcation on flanks is faint. Ears are grey-brown; feet are light (whitish or buffy) to blackish-brown; tail is usually distinctly bi-coloured, blackish-brown above, greyish-white below. Skull is relatively narrow (ZgW/CbL=0.50–0.60) with a long braincase; zygomatic arches are evenly bowed and the most exposed point is usually at the middle (Figure 206). Supratemporal ridges remain apart and although approach closely in the central interorbital region they never form a crest. At their anterior end the diverging ridges swell and form a depression in-between. The upper incisors protrude forward and are visible from above. Pattern of M_1 is fairly simple with 4 outer and 5 inner re-entrant angles; the anterior lingual angle LR5 is not deep. Triangle T5 is isolated from AC with a deep lingual re-entrant angle LR4 but there is usually (in 72% of voles from Russia; Lissovsky et al. 2018b) no complementary angle (BR4) on the buccal side. M^3 has

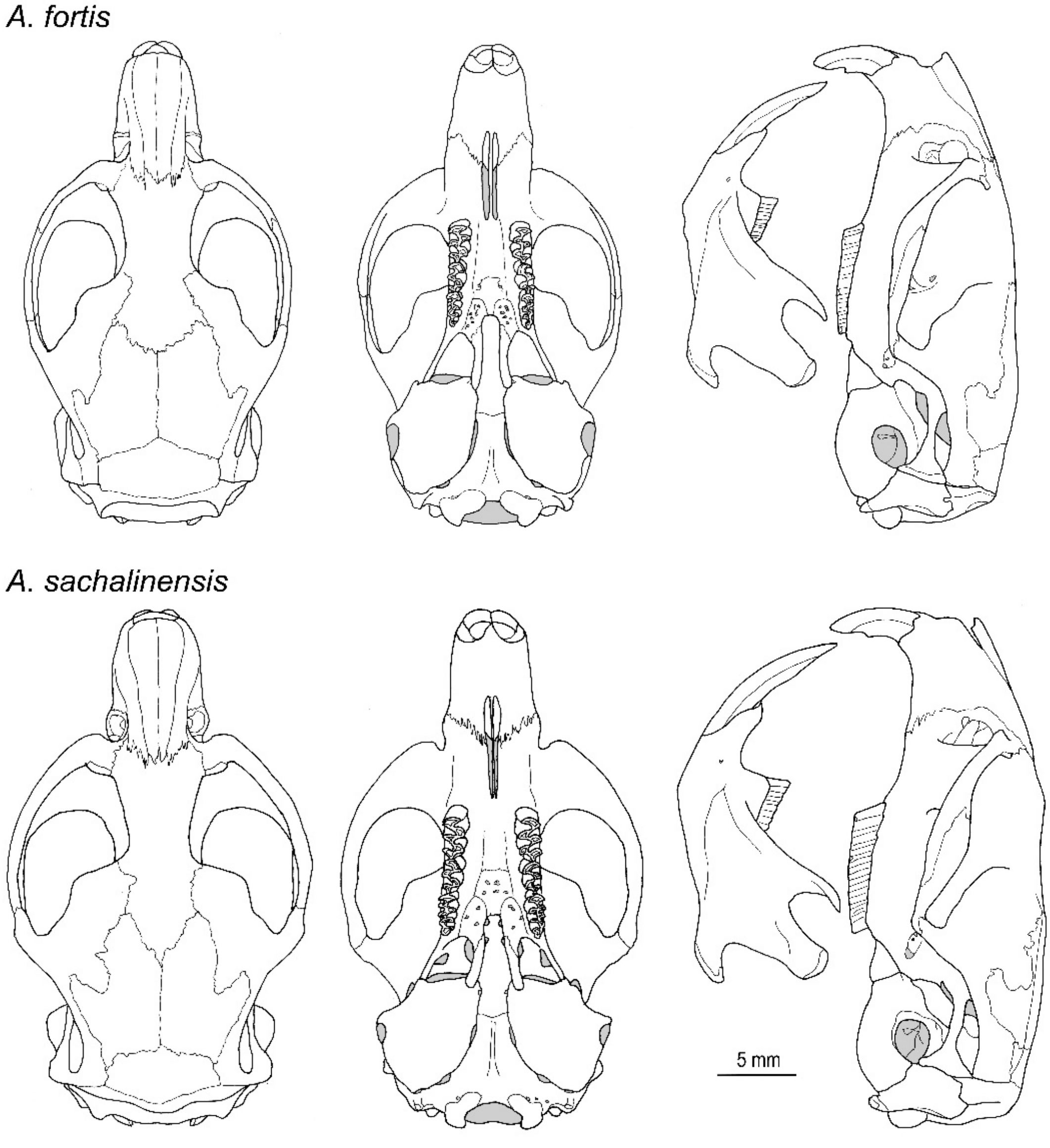


Figure 206: Skull and mandible of *Alexandromys fortis* from Buryatia, Russia (top) and *A. sachalinensis* (bottom).

4 inner and 3–4 (rarely 5) outer salient angles (Figure 207a,b).

Baculum is large and ossified; the proximal bone is 3.35–4.10 mm long and 1.66–2.50 mm wide; the point of greatest breadth is placed forward. The distal digits are slender; the central (length=0.90–1.55 mm) is 28% longer on average than the lateral digit (0.70–1.25 mm) (Aksenova & Tarasov 1974, Aksenova 1980). The sperm head is falciform; length×width=7.24×3.57 µm (Aksenova 1978, Orlov et al. 1974). Karyotype: 2n=52, NF_a=62 (Kovalskaya et al. 1988, Levenkova et al. 1997); ssp. *michnoi* has 6 pairs of submetacentrics and 19 pairs of acrocentrics (Orlov et al. 1978). The X chromosome is a large submetacentric, Y is a small acrocentric.

Variation and subspecies. The majority of authors list 5–6 subspecies (Luo et al. 2000, Shenbrot & Krasnov 2005). The subspecific variation has yet to be thoroughly assessed. A phylogenetic tree constructed from the *Mt*-DNA similarity matrix retrieved 3 major allopatric lineages. The most divergent (divergence time≈0.77 Mya) is an unnamed lineage from Linchuan County (Guangxi Province) on the southern distribution border. A further 2 lineages, the Southern (*calamorum* and *fujianensis*) and the Northern (the remaining subspecies) presumably diverged ~0.64 Mya and are separated by the Wiling Mts. and the Huaihe River (Gao et al. 2017). The molecular clock estimates do not match the estimated divergence between *fortis* and *limnophilus* (0.61±0.12 Mya; Bannikova et al. 2010).

Alexandromys fortis fortis (Büchner, 1889)

Microtus fortis Büchner, 1889:99. Type locality: "Ordos"; restricted by designation of the lectotype (Gromov & Baranova 1981:208) to "Khuankhe valley, Ordos (Inner Mongolia, China)" (Baranova & Gromov 2003:74).

Synonyms. *Microtus calamorum superus* Thomas, 1911.

Distribution. Central China in the great bend of the Huang He River (southern Nei Mongol, Ningxia, Shaanxi and western Gansu).

Characteristics. A large and long-tailed (TL/H&B=0.35–0.54) subspecies. Dimensions: BWt=52–113 g, H&B=115–170 mm, TL=48–67 mm, HF=21–25 mm, EL=13–16 mm, CbL=28.3–34.6 mm, ZgW=14.6–19.0 mm, MxT=7.0–8.2 mm. Dorsal pelage bright-tawny or buffy, belly washed buffy, hind feet whitish or buffy. Zygomatic arches moderately expanded (ZgW/CbL=0.51–0.58).

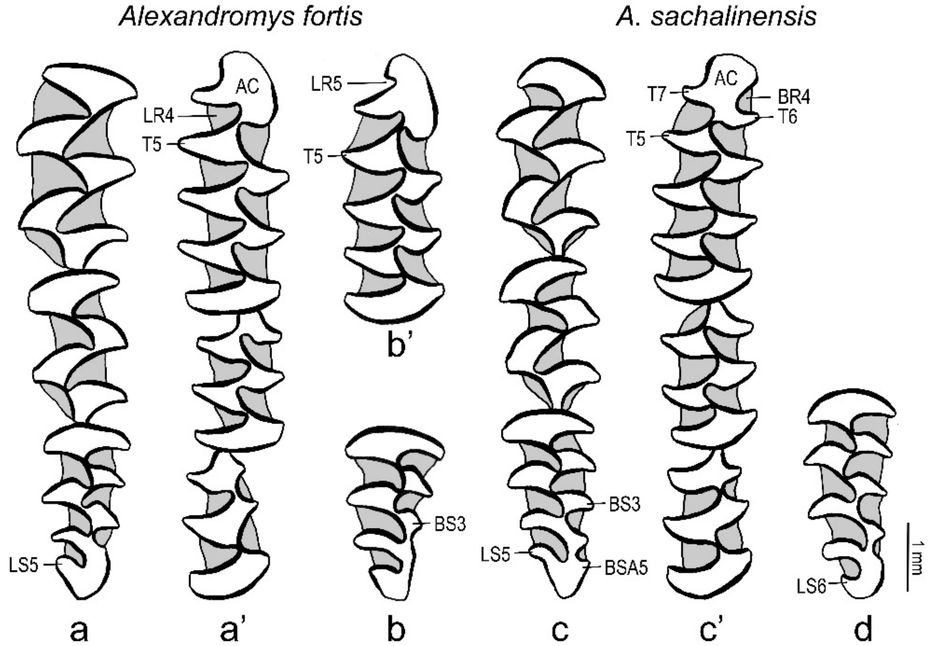


Figure 207: Molar pattern in *Alexandromys fortis* and *A. sachalinensis*. *Alexandromys fortis*: upper (a) and lower row (a') in a specimen from Kuantun, China; isolated M^3 (b) and M_1 (b'–Onsupiong, North Korea). *A. sachalinensis*: upper (c) and lower row (c'); isolated M^3 (d).

Alexandromys fortis calamorum (Thomas, 1902)

Microtus calamorum Thomas, 1902:167. Type locality: "Lower Yangtse [Yangtze River], near Nanking [Nanjing]. Sea level. (Type taken on the north bank)" (p. 168), China.

Distribution. This little known subspecies (cf. Luo et al. 2000) occupies the lower and middle reaches of the Yangtze River in southern China (Shandong, Anhui, Jiangsu, Sichuan, Hunan, Guangxi, Jiangxi and Zhejiang); in the opinion of Wang (2003) it is also present in Shanghai and Hubei (China).

Characteristics. A small and long-tailed subspecies (TL/H&B=0.38–0.42). Dimensions: H&B=127–139 mm, TL=53 mm, HF=21–23 mm, EL=14 mm, CbL=26.8–29.7 mm, ZgW=15.5–17.2 mm, MxT=5.6–7.6 mm. Dorsal pelage dark brown, sides of nose, rump and hips slightly washed fulvous, belly whitish, feet dull-brown. Zygomatic arches widely expanded (ZgW/CbL=0.57–0.58).

Alexandromys fortis michnoi (Kastchenko, 1910)

Microtus michnoi Kashchenko, 1910:288. Type locality by subsequent restriction: "Duriony … on the River Chikoim [Chikoy] 50 kilometers east of Troizkosavsk" (Vinogradov & Obolensky 1927:233) in the Kyakhtinskiy Raion, Republic of Buryatia, Russia.

Synonyms. *Microtus pelliceus* Thomas, 1911.

Taxonomy. Many authors (Luo et al. 2000, Wang 2003, Lunde 2008) held *pelliceus* as a separate subspecies. Allen (1940:860) concluded that *michnoi* and *pelliceus* are "doubtfully distinct" and Meyer (1978) synonymised the two. Rarely, *pelliceus* was synonymised with *maximowiczii* (Kuznetsov 1965).

Distribution. Russian part of the species range, northern Mongolia and north-eastern China, specifically north-eastern Hulun Buir Meng (northern Nei Mongol), Jilin, and Heilongjiang (Wang 2003); extreme north-eastern Korea (Jones & Johnson 1955).

Characteristics. Size and relative length of tail (TL/H&B=0.35–0.56) as in the nominal subspecies. Dimensions: BWt=52–101 g, H&B=120–165 mm, TL=40–93 mm, HF=18–25 mm, EL=12–18 mm, CbL=28.5–34.7 mm, ZgW=15.1–19.5 mm, MxT=7.0–9.2 mm. Dorsal pelage tawny to dark brown, grizzled by buffy hair tips; tawny individuals have buffy flanks; belly is grey, washed whitish (not buffy) and clouded by slate underhair. Feet are dark-brown to blackish-brown. Zygomatic arches moderately expanded (ZgW/CbL=0.51–0.58). No differences were observed on C-stained chromosomes between voles from Baikal, north-eastern Mongolia, and Russian Far East (Koval'skaya et al. 1991). Insular populations from the Peter the Great Bay (Sea of Japan) are approximately the same size as those from the mainland (Sheremetyeva 2017).

Alexandromys fortis dolichocephalus (Mori, 1930)

Microtus dolichocephalus Mori, 1930a:420. Type locality: "Cheng-chia-tun [subsequently spelled Chengchia-tun or Chengchiatun, now Shuangliao], Central Manchuria", Jilin Province, China.

Taxonomy. Sometimes synonymised with *pelliceus* (Won 1967) in the belief that *dolichocephalus* was based on immature individuals (Tokuda 1941).

Distribution. North-eastern China (Jilin and Liaoning); according to Wang (2003) also Tongliao (Nei Mongol).

Characteristics. A small and short-tailed (TL/H&B=0.31–0.44) subspecies. Dimensions: BWt=24–38 g, H&B=125–140 mm, TL=40–55 mm, HF=18.5–22 mm, EL=11–18 mm, CbL=28.0–31.2 mm, ZgW=15.0–16.0 mm, MxT=6.9–7.4 mm. Dorsal pelage is brown or cinnamon brown, underparts are light buffy to deep grey; cheeks, inner surface of ears and paws are whitish to light yellowish-brown (Mori 1930a, 1939). Skull narrow across zygomatic arches (ZgW/CbL=0.50–0.54).

Alexandromys fortis uliginosus (Jones & Jonson, 1955)

Microtus fortis uliginosus Jones & Johnson, 1955:193. Type locality: "Chip'o-ri (38° 08' N, 127° 19' E), [South] Korea".

Taxonomy. Won (1967) synonymised *uliginosus* with *pelliceus* [=*michnoi*].

Distribution. Central Korean Peninsula between Kumhwa and Ch'orwon (38°S parallel) (Jones & Jonson 1955). Jo et al. (2018:Fig.120) extended the range of *fortis* to the southern tip of the peninsula.

Characteristics. Similar to *michnoi* but larger: BWt=62–82 g, H&B=130–162 mm, TL=46–69 mm, HF=21–27 mm, EL=13–18 mm, CbL=32.8–35.0 mm, ZgW=18.3–19.7 mm, MxT=7.9–9.0 mm. Dorsal pelage shiny olive-brown, more ochraceous than *michnoi*; sides suffused with ochraceous, underside greyish-white and faintly tinged with buff, darker than *calamorum*. Tail is distinctly bi-coloured, blackish-brown above, greyish-white below. Skull is large and massive; zygomatic arches moderately expanded (ZgW/CbL=0.54–0.58).

Alexandromys fortis fujianensis (Hong, 1981)

Microtis fortis fujianensis Hong, 1981:444. Type locality: "Jianyang County, Fujian", China.

Distribution. River basins of Jianxi and Futunxi (upper reaches of the Min Jiang River), Fujian, south-eastern China (Luo et al. 2000).

Characteristics. Large subspecies: BWt=45–144 g, H&B=111–180 mm, TL=49–75 mm, HF=18–26 mm, EL=8–18 mm, CbL=30.9–36.1 mm, ZgW=17.8–20.0 mm, MxT=7.9–9.3 mm (Luo et al. 2000). Dorsal pelage and tail are dark brown, belly is grey and washed buff; front paws are light grey-brown, hind paws are dark brown. Zygomatic arches widely expanded (ZgW/CbL=0.54–0.60).

Species group *maximowiczii*

Taxonomy. The group is genetically (Steppan & Schenk 2017) and morphologically (Aksenova 1980) well-defined. The 3 species (*maximowiczii, evoronensis, mujanensis*) are characterised by a wide intraspecific variation of chromosomal features interpreted as a sign of on-going speciation (Lemskaya et al. 2015). Pairwise genetic distances are low (2.7–2.9%) and in the *Mt*-trees *maximowiczii* is paraphyletic with respect to *evoronensis* and *mujanensis* (Haring et al. 2011, Bannikova et al. 2019). Most authors keep these three taxa as distinct species, however, Lissovsky et al. (2018a) ranked *evoronensis* and *mujanensis* as a subspecies of *maximowiczii* or merely as cytotypes of a chromosomally polymorphic *maximowiczii* (Lissovsky et al. 2019). Meyer et al. (1996) showed that F1 hybrids between these taxa are invariably sterile, which caused us to keep *mujanensis* and *evoronensis* as two independent species. The closest relative to the *maximowiczii* group is not known with certainty. *Mt*-sequences suggest it is *sachalinensis* (Frisman et al. 2009, Bannikova et al. 2010, Haring et al. 2011) which concurs with an earlier view from Meyer et al (1996); a multigenic approach points to *oeconomus* (Lissovsky et al. 2018a).

Distribution. Eastern Asia between Lake Baikal and the upper course of the Yellow River; also Sakhalin.

Characteristics. Large, moderately long-tailed and dark grass voles; interdigital pads 2–4 larger than the medial metatarsal pad. M_1 with deep antero-buccal re-entrant angle BR4. Sperm head is semi-oval with the acrosome on its apex.

Alexandromys sachalinensis (Vasin, 1955) – Sakhalin Grass Vole

Microtus sachalinensis Vasin, 1955:427. Type locality: "on Sakhalin [Island] in Poronaytsk rayon, on the left bank of Oleney R. [Olenya River] at its mouth to L[ake] Nevskoe (Tarayka)", Russian Federation.

Taxonomy. *A. sachalinensis* was rarely synonymised with *fortis* (as *maximowiczii pelliceus*; Reimers 1972) or *oeconomus* (Kuzyakin 1963, Kuznetsov 1965). Evidence confirming its species status emerged during the 1970s (summarised in Meyer 1978). Possibly a close relative of *fortis* or *maximowiczii* (Pozdnyakov 1993, Meyer et al. 1996, Bannikova et al. 2010).

Distribution. (Figure 208). Endemic to Sakhalin where they occupy an area of ~6,300 km^2 on the northern and central parts of the island (as far south as ~49th northern parallel). Live in swamps and peat bogs in depressions from sea level up to 104 m a.s.l.

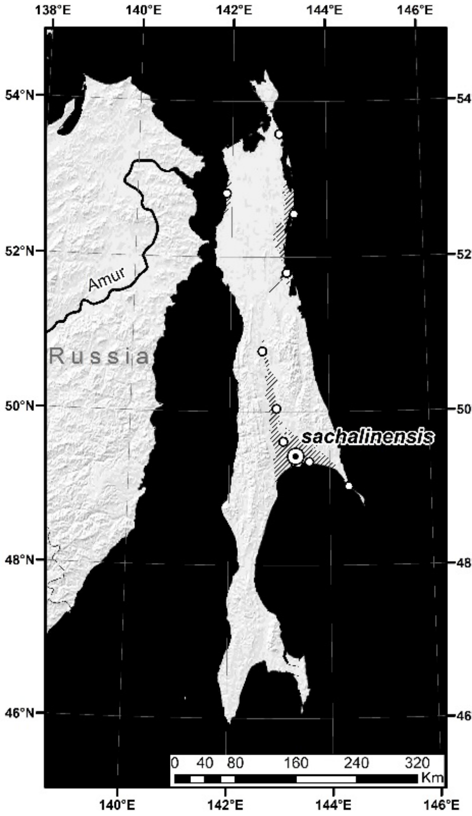


Figure 208: Distributional range of the Sakhalin grass vole *Alexandromys sachalinensis*.

Characteristics. Size and external appearance as in *fortis* but the tail is comparatively shorter (TL/H&B=0.26–0.44). Dimensions: BWt=51–155 g, H&B=124–175 mm, TL=35–69 mm, HF=21–29 mm, EL=12–19 mm, CbL=29.5–36.0 mm, ZgW=16.4–20.8 mm, MxT=7.5–8.8 mm. There are 5 plantar pads (6 in 15.4% of voles; Meyer et al. 1996) which are of approximately the same size. On the front paw the interdigital pads are smaller than the metacarpal pads; plantar pads are approximately identical in size. Ears are fairly long, overtopping the fur. Fur is soft, 8–10 mm long; length of sparse long hair=10–14 mm. Back is dull russet, grizzled by buffy tipped hairs; dull tints predominate. Flanks are more drab, underside is grey, grizzled by whitish hair tips; feet are brownish-grey and ears are grey. Tail is indistinctly bi-chromatic in the majority of voles, blackish-brown above, grey below; densely hairy throughout and the terminal pencil measures 6–8 mm. Skull resembles *fortis* in proportions but is more ridged and shallower (height of skull behind M^3 as percent of CbL frequently <35% vs >35% in *fortis*). Dorsal profile is flat or slightly concave (Figure 206). The interorbital crest is rather low and short, splitting towards the lacrimals; posteriorly, the crest diverges abruptly close to the parietals. The depression between the anterior ridges is smaller and shallower than in *fortis* but is present in ~20% of adult skulls (Lissovsky et al. 2018b). The alveolar process of the mandible is modest. On the M_1 the antero-lingual triangle T5 is closed; T6–T7 widely open into the AC; the antero-buccal re-entrant angle BR4 is usually deep and only exceptionally obtuse; the shape of the anteroconid complex is remarkably stable. M^3 is more complex than in *fortis* with 5 (rarely 4) salient angles on either side; the posteriormost outer angles are invariably small (Figure 207c,d). The proximal baculum is shorter than in *fortis* (length=2.60–3.50 mm, greatest width=1.10–2.20 mm) but the medial distal baculum is comparatively longer (1.30–2.00 mm). The distal baculum therefore makes up on average ~57% the length of the proximal baculum (vs. 34% in *fortis*). Lateral digits are slightly shorter than in *fortis* (0.60–1.20 mm), i.e. on average equalling 53% the length of the proximal baculum (78% in *fortis*) (Aksenova & Tarasov 1974, Aksenova 1980). The sperm head is oval with a conical acrosome situated at the top of the nucleus; the head is larger than in *fortis*: length×width=7.83×5.00 μm (Aksenova 1978). Karyotype: 2n=50, NF_a=62; X is metacentric and Y is small acrocentric. The majority of autosomes are acrocentric as in *fortis* (Meyer 1978).

Variation and subspecies. A monotypic species.

Alexandromys maximowiczii (Schrenck, 1859) – Maximowicz's Grass Vole

Taxonomy. For many years known under the name *ungurensis*. The name *maximowiczii* was accepted by

Sowerby (1923) but was considered to be nomen dubium (Ellerman & Morrison-Scott 1951) and entered into general use only with Ognev (1950). Heptner & Shvetsov (1960) merged *maximowiczii* with *fortis*; until recently, *maximowiczii* included *gromovi* (e.g. Musser & Carleton 2005) which was described as its subspecies but is now in *shantaricus*. Kuzyakin (1963) regarded *maximowiczii* as a subspecies of *oeconomus*.

Distribution (Figure 209). The range (area=1,134,000 km²) covers Buryatiya and Zabaykalskiy Krai (Russia), Selenge, Hentiy and Tov (Mongolia), the Amur Valley as far as 250 km downstream from its confluence with the Ussuri (the border zone between China and Russia), eastern and north-eastern Nei Mongol, Heilongjiang, Jilin, northern Hebei (China), and Dormod in eastern Mongolia. Small isolates are scattered further west in Arhangay (Mongolia) and southern Nei Mongol, southern Hebei and Shaanxi (China). The western border is defined by the Lake Baikal–Ordos loop (the Yellow River), the eastern border is on the lower Amur and Ussuri; the northern boundary lies on the Tsypa River (Buryatia) and the Zeya River (Amur Region). Principal habitats are marshy meadows of grasses and sedges, heathland and bogs in riverine valleys, in sparse woodland and in the uplands at altitudes of 15–1,900 m. Wherever it is sympatric with *fortis, maximowiczii* occupies less dump sites (Dymin 1974).

Characteristics. Moderately large grass vole with tail slightly shorter than in *fortis* (TL/H&B=0.28–0.42); sparse hairs do not conceal the tail annulation and the terminal pencil is moderately long (6.5–9 mm). Ears are hidden in the fur. There are 5 plantar pads (6 pads in 18.3% of cases; Meyer et al. 1996); the medial metatarsal pad is small and placed close to the postero-medial interdigital pad (Figure 204b). Hair is soft, 8–11 mm long on the midback, but sparse hairs are longer (up to 17.5 mm). Dorsal pelage is dull russet to dark brown, grizzled by yellowish hair tips; buffy tints are rare. Flanks have more of either a buffy or grey stain; demarcation between the light grey belly and the back is rather distinct. Tail is either uniformly blackish-brown or

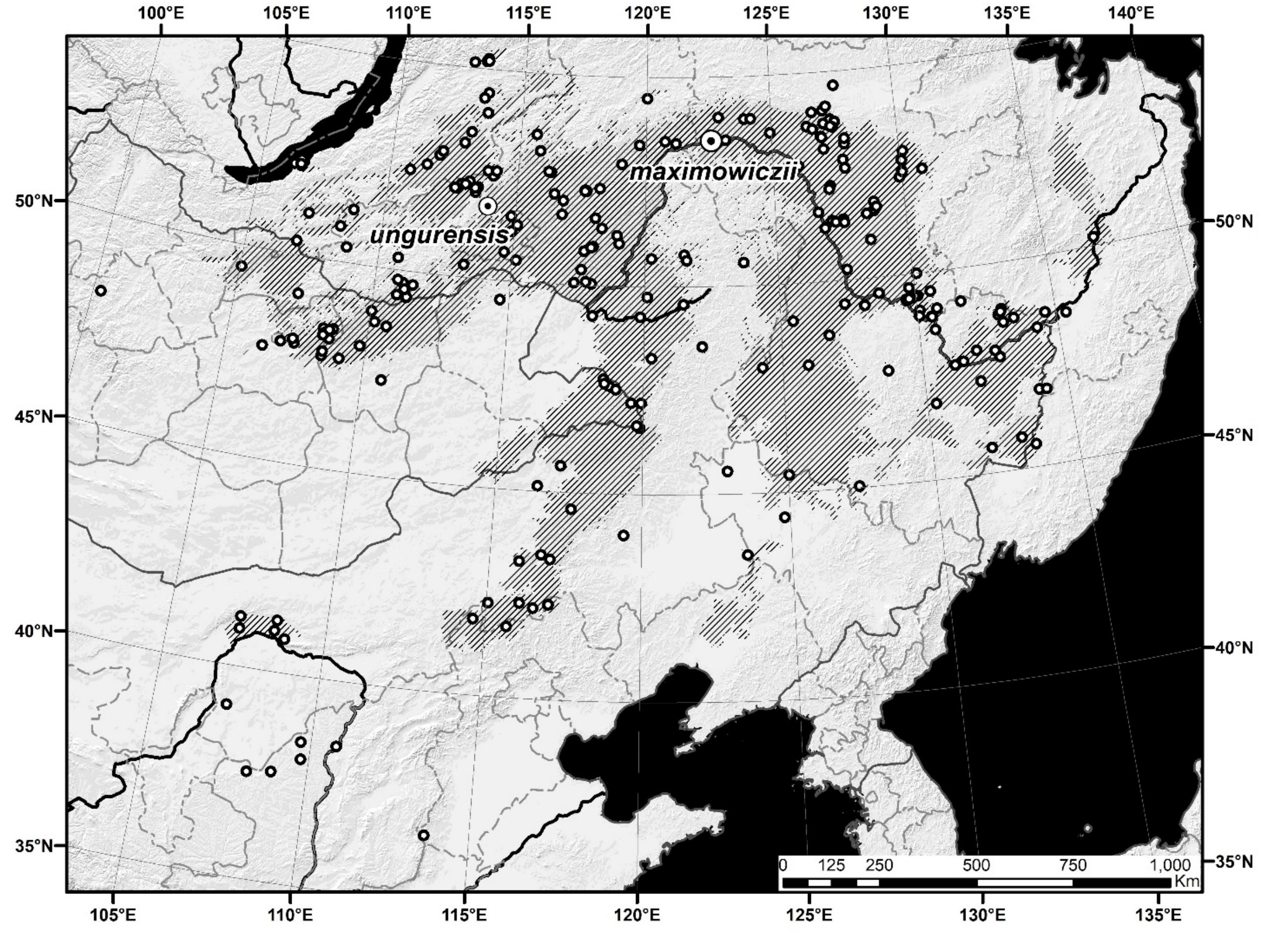
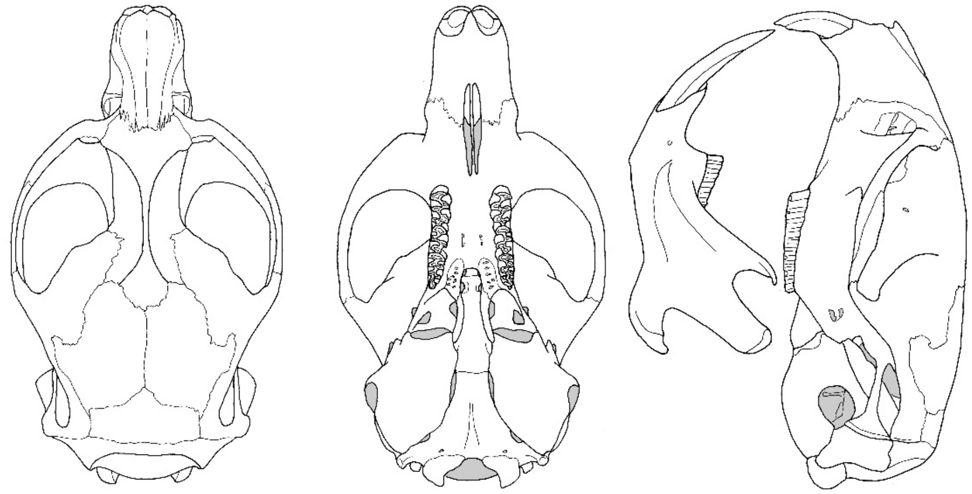
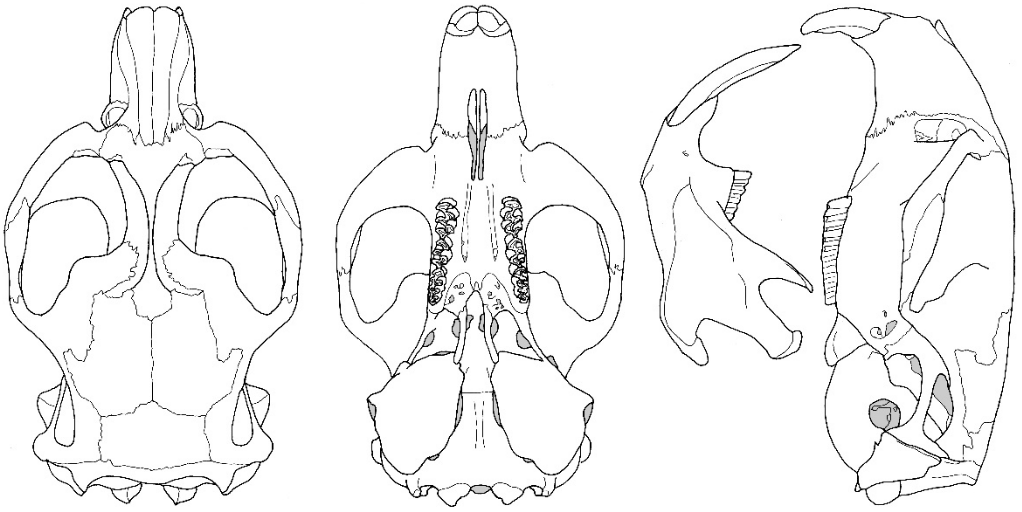


Figure 209: Distributional range of Maximowicz's grass vole *Alexandromys maximowiczii.*

A. maximowiczii



A. mujanensis



A. evoronensis

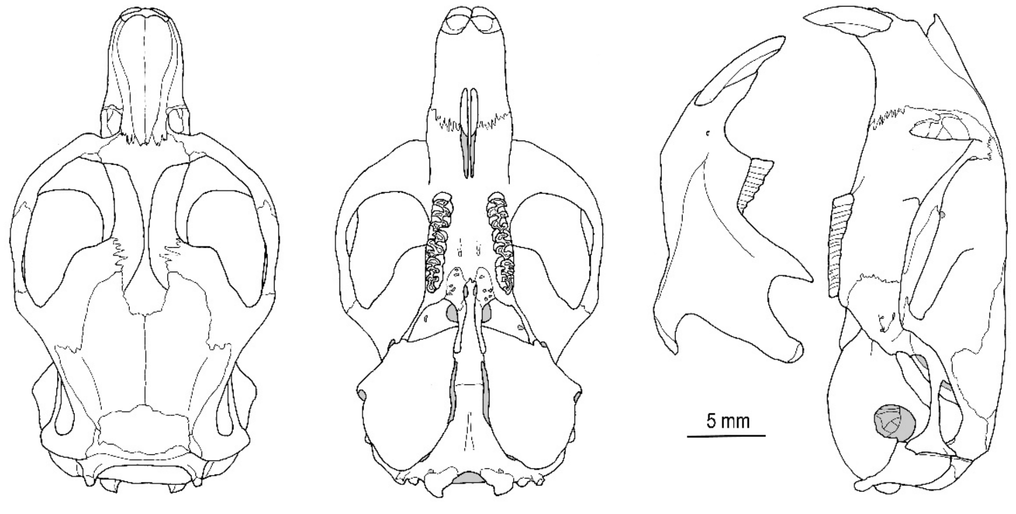


Figure 210: Skull and mandible of grass voles from the species group *maximowiczii* (top to bottom): *Alexandromys maximowiczii* (Amurskaya Oblast, Russia; top), *A. mujanensis* (Muya Depression, Russia; middle) and *A. evoronensis* (Evoron, Khabarovsky Krai, Russia; bottom).

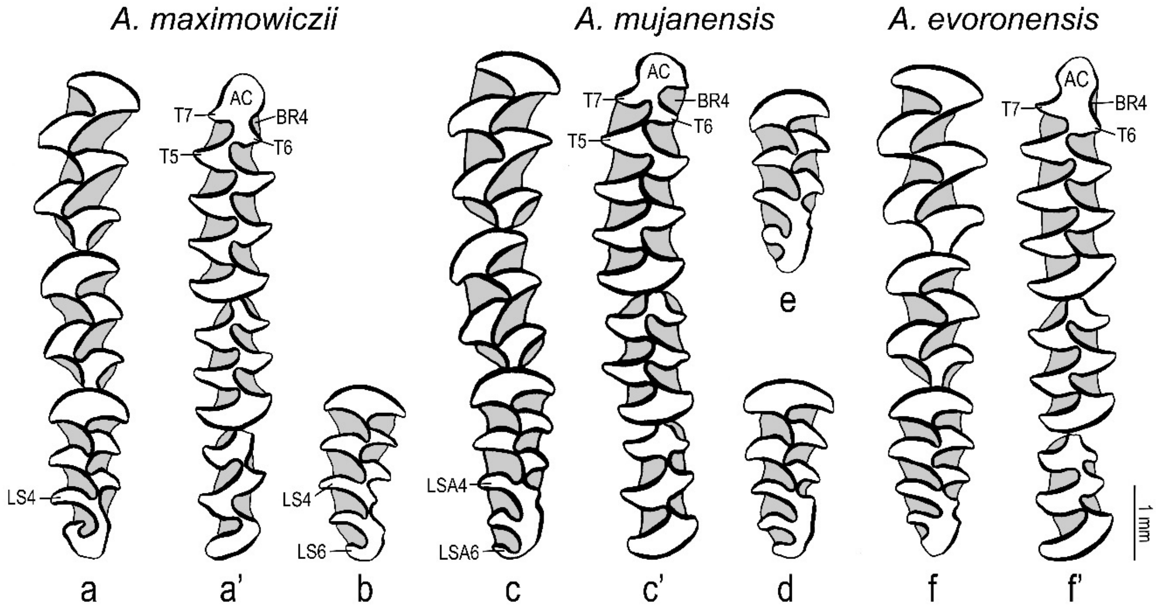


Figure 211: Molar pattern in grass voles from the *maximowiczii* species group. *Alexandromys maximowiczii*: upper (a) and lower row (a'–vicinity of Kiker, Olja District, Transbaikal Russia); isolated M^3 (b–Khabarovsky Krai, Russia). *M. mujanensis*: upper (c) and lower row (c'–Muya Depression, Buryatia, Russia); isolated M^3 (d,e–Muya Valley, Russia). *A. evoronensis*: upper (f) and lower row (f').

indistinctly bi-coloured (light-grey below); feet and ears are dark, usually blackish-brown. Young are dull brown with a dark grey belly and uniformly dark tail. Skull shows similar outline as in *fortis* (ZyB/CbL=0.51–0.58). In adult skulls (age>3 months), the supratemporal ridges merge into a crest in the mid-orbital region; the ridges diverge at their anterior end towards the lacrimals and on the posterior side just before the parietals (Figure 210). M_1 is more complex than in *fortis*: T5 is always closed, the antero-labial re-entrant angle BR4 is usually present and deep (absent in <20% of individuals). The AC is well-defined although widely confluent with triangles T6–7. M^3 has 4 (rarely 3 or 5) salient angles on the lingual side and 3 (rarely 4–5) salient angles on the labial side (Figure 211a,b). Baculum is slightly shorter than in *fortis* (length of the proximal bone=2.85–3.85 mm) and narrower at its base (width=1.50–2.55 mm). The central distal digit is longer on average (1.00–1.85 mm) but the lateral digits are decidedly shorter (0.60–1.00 mm; Aksenova & Tarasov 1974, Aksenova 1980). Sperm head (length×width=8.17×5.27 µm) is semi-oval with conical acrosome situated on the apex (Aksenova 1978, Orlov et al. 1974).

The karyotype is polymorphic (2n=36–44, NF=52–62) and contains 13–19 bi-armed and 18–30 acrocentric chromosomes; both heterosomes are acrocentric. Thus far, 5 chromosomal forms have been recognised (Orlov et al. 1978, Kovalskaja & Sokolov 1980, Kartavtseva et al. 2008, 2013): form A (2n=39–44, NF=53–60) in Buryatiya and Zabaykalskiy Krai; form B (2n=38–42, NF=54–57) from the shores of Lake Baikal and the estuary of Selenga; form C (2n=39–41, NF=55–60) from Central Amur; form D (2n=40–43, NF=54–58) from the upper Amur, eastern Mongolia and adjacent parts of Zabaykalskiy Krai; and form V (2n=36–40, NF=52–56) from the border zone between Zabaykalskiy Krai and Mongolia. The major mechanisms driving polymorphism are pericentric inversions, translocations and Robertsonian fusions.

Variation and subspecies. Regarded either as monotypic (Ognev 1950, Kostenko 1984, 2000) or containing 2 subspecies (Gromov & Erbajeva 1995, Shenbrot & Krasnov 2005). The latter view was endorsed from morphological and chromosomal evidence and follows below. Using a *Mt*-DNA control region, phylogeographic assessment retrieved a major division (=0.0282±0.0043%) in the western part of the range. The most distinct are B and V chromosomal forms (Sheremetyeva et al. 2015).

Alexandromys maximowiczii maximowiczii (Schrenck, 1859)

Arvicola maximowiczii Schrenck, 1859:140. Type locality: "Amur land"; restricted to "Amur Obl[ast], Skovorodinskiy r[ayon], r[iver] Omutnaya", Russia (Pavlinov & Rossolimo 1987:197).

Distribution. Russian Far East (as far west as the Amur-Songhua confluence), eastern Mongolia and north-eastern China.

Description. Dimensions: BWt=34–79 g, H&B=110–148 mm, TL=38–57 mm, HF=16–22 mm, EL=10–16 mm, CbL=26.5–30.2 mm, ZgW=14.2–17.3 mm, MxT=6.2–7.5 mm. Pelage is dark, rarely with a buffy tint. M^3 less complex, in ~70% of cases having 4 outer salient angles (Vorontsov et al. 1988). The shape of M_1 is closer to *evoronensis* and *mujanensis* than to *ungurensis* (Pozdnaykov 1993). Proximal and central distal baculum are longer ($\bar{x}$=3.56 mm and 1.69 mm, respectively) but the lateral digit is shorter ($\bar{x}$=0.75 mm). Basal expansion is wider ($\bar{x}$=2.34 mm; i.e. ≈66% of the length of the proximal baculum; Aksenova 1980) than in *ungurensis*. Contains chromosomal form C (Kartavtseva et al. 2008).

Alexandromys maximowiczii ungurensis (Kastschenko, 1913)

Microtus michnoi var. *ungurensis* Kashchenko, 1912:418. Type locality: "(Chitinskaya uezda [Chita County]), r[iver] Ungur, 10 versts [10.5km] from stanica [Cossac village] Makoveevo", Chita, Russia.

Distribution. Southern and eastern Buryatia, south-western Zabaykalskiy Krai, Russian Far East (the upper Amur as far east as its confluence with Songhua), and northern Mongolia.

Description. Dimensions: BWt=43–82 g, H&B=100–152 mm, TL=34–57 mm, HF=15–23 mm, EL=10–16 mm, CbL=26.2–30.8 mm, ZgW=14.4–17.0 mm, MxT=6.5–7.8 mm. Pelage, although variable, more commonly displays buffy tints. M^3 in 62% of cases more complex, with 5 outer salient angles (Vorontsov et al. 1988). Proximal and central distal baculum are shorter on average ($\bar{x}$=3.27 and 1.37 mm, respectively) but the lateral digit is longer ($\bar{x}$=0.86 mm). Basal expansion is narrower (mean=1.89 mm; i.e. ≈58% of the length of the proximal baculum; Aksenova 1980). Contains chromosomal forms A, B, D, and V (Kartavtseva et al. 2008).

Alexandromys mujanensis (Orlov & Kovalskaya, 1978) – Muya Grass Vole

Microtus mujanensis Orlov & Kovalskaya, 1978:1224. Type locality: "Bauntovski rayon, Buryat ASSR [now Buryat Republic], in a valley of Muya River (around village Muya), on a sedge-cereal meadow", Russian Federation.

Taxonomy. Retrieved as a distinct species on the basis of its karyotype and cross-breeding trials with *maximowiczii* (Orlov & Kovalskaya 1978, Golenishchev 1982). Lemskaya et al. (2015:241) hypothesised that *mujaensis* "could not originate earlier than 12,000 years ago".

Distribution (Figure 212). A small-range occupying ~3,615 km^2, endemic to the north-east of Lake Baikal, between the Barguzin Depression and the confluence of Muya and Vitim (Buryatiya and Zabaykalskiy Krai, Russia). Lives in swampy sedge meadows and birch-larch stands in floodplain river valleys and the bottoms of depressions (Borisova & Kartavtseva 2013). Altitudinal range is 460–1,070 m.

Description (Figure 202a). Dimensions: BWt=34–145 g, H&B=106–170 mm, TL=37–67 mm, HF=17.5–24 mm, EL=11.5–17.5 mm, CbL=28.0–35.4 mm, ZgW=15.1–20.0 mm, MxT=6.6–9.3 mm. Larger than *maximowiczii*, externally resembling *sachalinensis* (Golenishchev 1982). Tail rather short (TL/H&B=0.28–0.39), densely hairy; terminal pencil=6.5–9.5 mm. Ears overtop the fur; there are usually 5 plantar pads (6 in 22.8% of voles; Meyer et al. 1996). Pelage is soft, 8–13.5 mm long; the longer (12–17 mm) hairs are fairly dense. The back is dark brown (usually lighter than in *maximowiczii*), heavily grizzled by

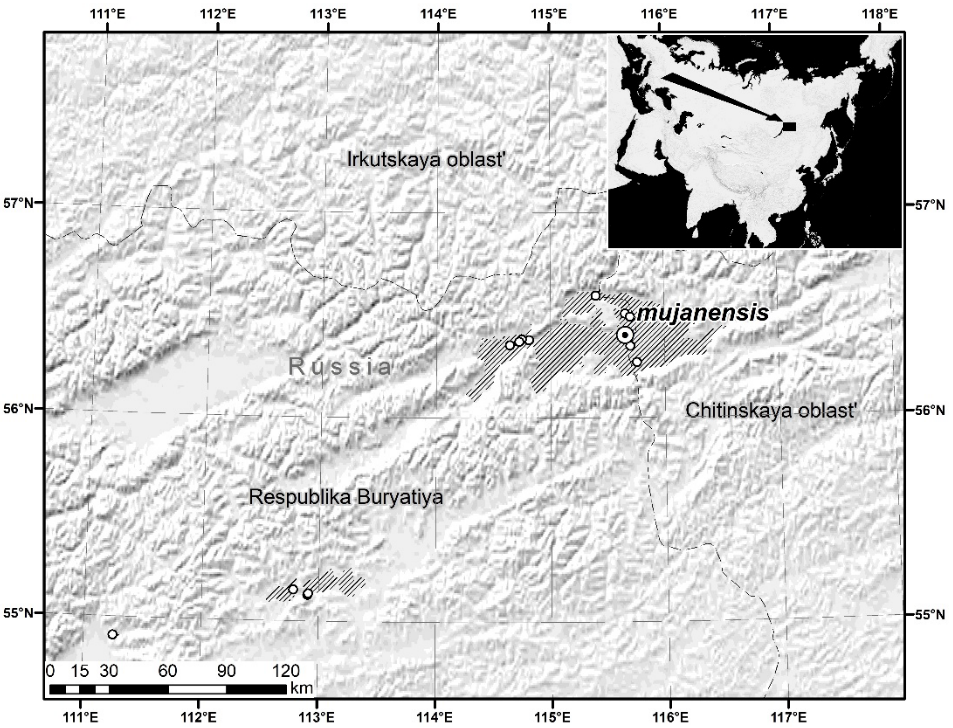


Figure 212: Distributional range of the Muya grass vole *Alexandromys mujanensis*.

buffy tips. The auricular region, cheeks, snout and hips are frequently light-rusty or buffy. Belly is invariably grey; the tail is indistinctly bi-coloured and rather dark. Skull as in *maximowiczii* (Figure 210); the supratemporal ridges are powerful, the squamosal processes are prominent. Zygomatic arches are heavy and moderately expanded (ZgB/CbL=0.53–0.59). Mandible shows no peculiarities; angular process is feeble. Molars are more complex than in *maximowiczii*. M^3 has 4–5 inner and 3–5 outer salient angles; morphotypes with 5 inner and 3–4 outer angles prevail. M^1 has 5 (rarely 6) inner and 4 (rarely 5) outer salient angles. Triangle T6 is normally confluent with T7 but is occasionally isolated by a deep antero-lingual re-entrant angle BR4 (Figure 211c'). Baculum is essentially as in *maximowiczii* but the central (length=1.5–2.3 mm) and the lateral (=1.0–1.6 mm) distal digits are longer. The sperm head (length×width=8.4×5.6 µm) is oval with a conical acrosome situated on the apex (Golenishchev 1982). The karyotype (2n=38) contains 4 polymorphic chromosome pairs which originated through pericentric inversions; NF_a=46–49. The X is submetacentric (always acrocentric in *maximowiczii*) and Y is acrocentric (Kartavtseva et al. 2019).

Variation and subspecies. Monotypic species. Genetic distances calculated from the *Mt*-DNA control region between the 3 population fragments are low (0.0166–0.0183%; Kartavtseva et al. 2019).

Alexandromys evoronensis (Kovalskaja & Sokolov, 1980) – Evoron Grass Vole

Microtus evoronensis Kovalskaja & Sokolov, 1980:1410. Type locality: "Selnochno rayon [Solnechnyy Raion], Khabarovsk Krai, on the shore of Lake Evoron at the estuary of Devyatka River, on a grassy meadow", Russian Federation.

Taxonomy. Retrieved as a species distinct from *maximowiczii* on the basis of its unique karyotype and cross-breeding trials (Kovalskaja & Sokolov 1980).

Distribution. (Figure 213). A small-range endemic (area=11,000 km^2); localities are widely scattered in the Amur Oblast (Arga and Tok Valleys, the Zeba River Basin) and in Khabarovsk Krai (watersheds of Amgun', Chegdomyn, Odon, Devyatka and Nimelen Rivers), Russian Far East. Lives in hummocky meadows and reed beds in regularly flooded plains (Kostenko 2000). Altitudinal range is 63–352 m.

Description. Dimensions: BWt=51–91 g, H&B=130–155 mm, TL=40–55 mm, HF=18–21.4 mm, EL=12.1–

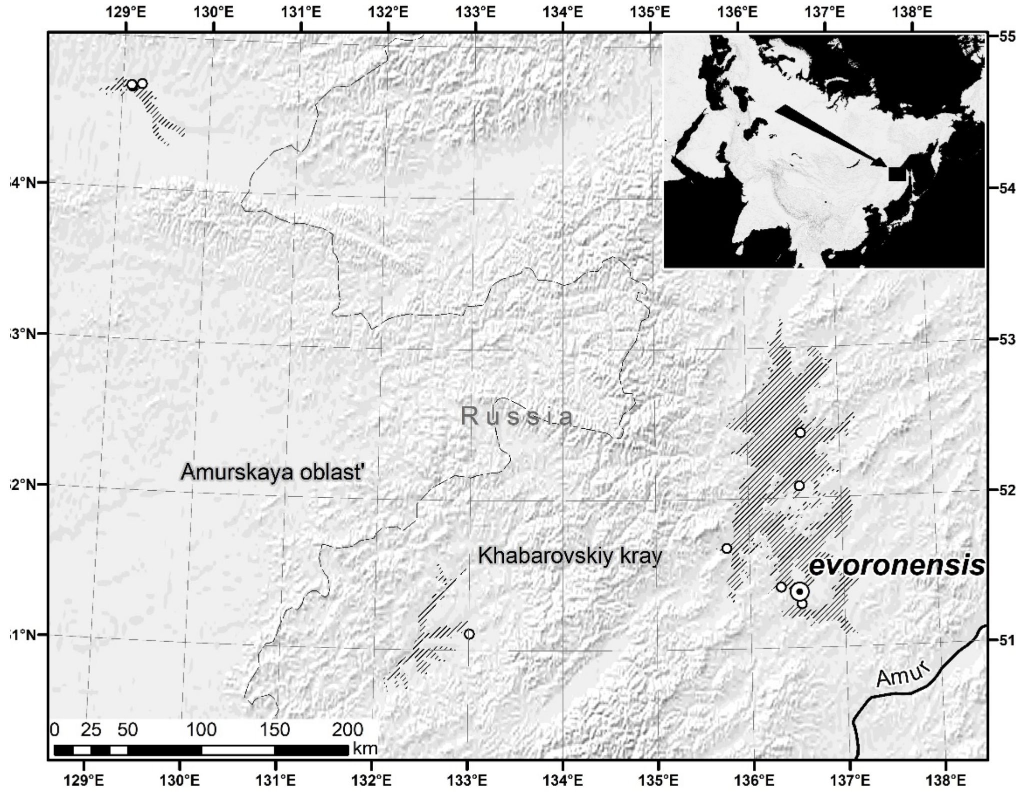


Figure 213: Distributional range of the Evoron grass vole *Alexandromys evoronensis*.

15.3 mm, CbL=29.1–32.8 mm, ZgW=16.2–18.4 mm, MxT=6.8–8.0 mm. Size and relative length of tail (TL/H&B=0.29–0.39) as in *mujanensis*; ears barely protrude above the fur. Usually there are 5 plantar pads (6 pads in 14.3% of voles; Meyer et al. 1996), their configuration is as in *maximowiczii*. The tail is densely hairy with a prominent pencil (length=7–11 mm). Fur is soft; hairs are 7–11 mm long; protruding hairs measure 10–13.5 mm. Dorsal pelage is dark brown, heavily grizzled by buffy hair tips; in some voles the buffy shade becomes more intense on the flanks. Underside is grey to silvery, distinctly demarcated from the back. Ears and paws are blackish-grey; tail is blackish-brown all around, slightly darker above. Skull and molar pattern is the same as in *mujanensis* (Figures 210, 211f). M^3 has 4–5 inner and 3–4 (rarely 5) outer salient angles; M^1 is with 5 (rarely 4) inner and 4 outer re-entrant angles. Baculum is as in *mujanensis* except that the lateral distal digits are as short (=0.65–1.00 mm) as in *maximowiczii*. Sperm head indistinguishable from *mujanensis* or *maximowiczii* (Kovalskaja & Sokolov 1980). The karyotype is polymorphic: 2n=36–41, NF=51–59; the X chromosome is submetacentric and the Y is acrocentric (Meyer et al. 1996, Sheremetyeva et al. 2017, Kartavtseva et al. 2021a,b).

Variation and subspecies. Monotypic species.

Species group *mongolicus*

Taxonomy. Grass voles, classified here in the *mongolicus* group (*mongolicus, alpinus, middendorffii* and *shantaricus*), were never previously considered taxonomically close. E.g. *mongolicus* was in the subgenus *Microtus* for many years, *shantaricus* was described as a subspecies of *oeconomus*, and *middendorffii* was even classified in *Stenocranius* (Chaline & Mein 1979). Close affinities among these species were fully revealed only from the molecular trees (Bannikova et al. 2010, 2019). Lissovsky et al. (2018a), who named the group "short-tailed voles", tacitly ranked all its taxa as conspecific. We follow Bannikova et al. (2019) who classified *mongolicus, alpinus, middendorffii* and *shantaricus* as distinct species which putatively diverged ~320–380 kya (Bannikova et al. 2010).

Distribution. The group is widespread in polar and boreal Asia, between the Kara Sea in the west and the Pacific Ocean in the east, and from the Arctic Ocean in the north till the 42nd parallel in the south.

Characteristics. Small to moderately large voles with a proportionally short tail. Skull is rather small and delicate, temporal ridges frequently stay apart; sagittal crest is usually short. Sperm head is semi-oval with conical acrosome situated on the apex.

Alexandromys mongolicus (Radde, 1861) – Mongolian Grass Vole

Arvicola mongolicus Radde, 1861:681. Type locality: "Torey-nor" i.e. "a system of Torey Lakes, Borzinskiy rayon, Chita Oblast", Russia (Baranova & Gromov 2003:78).

Synonyms. *Microtus (Arvicola) poljakowi* Kashchenko, 1901; *Microtus xerophylus* Skalon, 1936.

Taxonomy and nomenclature. For most of the 20th century *mongolicus* was regarded as a species in its own right but was synonymised with *arvalis* in the 1950s. The taxonomic singularity of these voles has become obvious since the late 1960s from cross-breeding trials and chromosomal analyses (Malygin 1978, Orlov et al. 1978, Schvetsov et al. 1981). Throughout that period, *mongolicus* was kept in the subgenus *Microtus*, either in the *mongolicus* species group as its sole member (Radjabli et al. 1984) or in the *arvalis* species group (e.g. Meyer et al. 1996). For relationships with *alpinus* see under that species. Allen (1924, 1940) reported Mongolian grass voles under 3 names: *mongolicus, poljakowi* (synonymised with *mongolicus* already by Vinogradov & Obolensky 1927) and *obscurus*.

Radde denoted *mongolicus* as a new name twice, in 1861 and 1862, therefore the date of publication is frequently incorrectly quoted as 1862.

Distribution (Figure 214). The range covers an area of 529,690 km^2 and is spread between the Selenga River in the west and the Ussuri in the east, encompassing the trans-Baikal region (in Buryatiya, Aginskiy Buryatsky Autonomous Oblast, and Zabaykalskiy Krai) and the Far East (Amur Oblast) in Russia, eastern Mongolia (districts of Bulgan, Dornod, Hentiy, Selenge, and Tov) and north-eastern China (Heilongjiang, Jilin, and Nei Mongol). Lives in humid meadows and sparse thickets in riverine valleys and on lakeshores; rarely found in dry open landscape, in marshes and reeds (Vinogradov & Obolensky 1927, Bannikov 1954, Xu 2016). Altitudinal range is 40–2,700 m.

Characteristics (Figure 202d). A grass vole of moderate size: BWt=20–53 g, H&B=93–142 mm, TL=24–53 mm, HF=13–20 mm, EL=9–13.5 mm, CbL=23.0–30.0 mm, ZgW=12.8–16.9 mm, MxT=5.3–

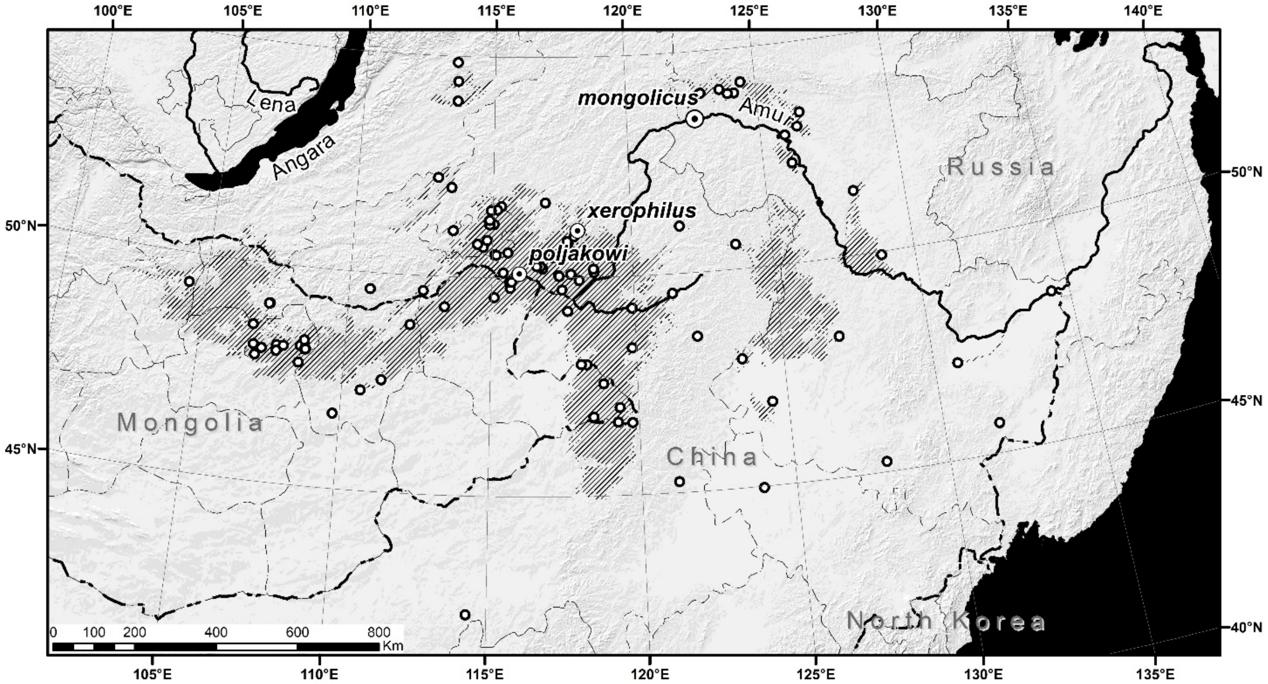


Figure 214: Distributional range of the Mongolian grass vole *Alexandromys mongolicus*.

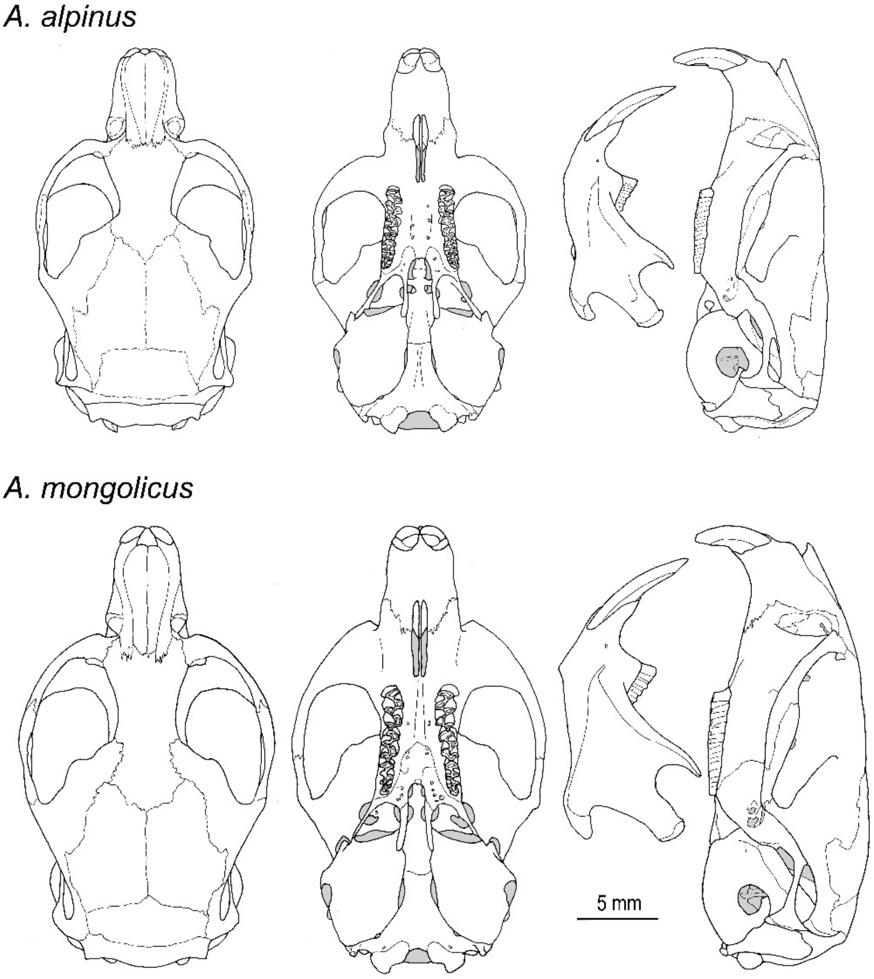


Figure 215: Skull and mandible in *Alexandromys alpinus* (Khangai Mts., Mongolia; top) and *A. mongolicus* (Yalu, Nei-Mongol, China; bottom).

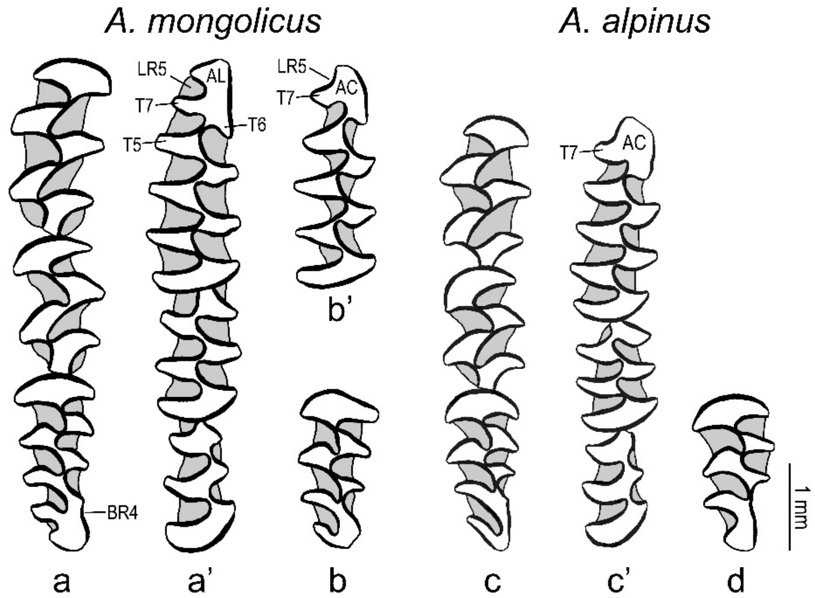


Figure 216: Molar pattern in *Alexandromys mongolicus* and *A. alpinus*. *A. mongolicus*: upper (a) and lower row (a'–upper flows of the Karganashi River, Trans-Baikal, Russian Federation); isolated M^3 (b) and M_1 (b'–Torei Nor, Amur Oblast, Russia). *A. alpinus*: upper (c) and lower row (c') and isolated M_3 (e'–Khangai Mts., Mongolia).

7.5 mm. Tail is rather short (TL/H&B=0.24–0.38) and densely clothed in hair which terminates in ~8 mm long pencil. Eyes are modestly large and the ears just overtop the fur. There are 5 plantar pads (in 83% of individuals; Meyer et al. 1996).

The medial metatarsal pad is smaller than the interdigital pads 2–4. The front thumb has a claw. Fur is rather harsh and short (length=6–7 mm; sparse protruding hairs up to 11 mm), dark brown and grizzled buffy by light hair tips on the dorsal side. Pelage is lighter and with buff shades on the frontal, temporal and buccal regions. Flanks are suffused grey; the underside is grey, demarcation is rather obvious. Paws are brownish-grey, ears are grey and tail is sharply bi-coloured (blackish-grey above and grey below). The skull is of average proportions (Figure 215); zygomatic arches are evenly bowed and not particularly expanded (ZgW/CbL=0.52–0.59). The nasals are short and terminate well before reaching the level of incisors. Supratemporal ridges are present in adults but only rarely merge into a short sagittal crest which starts behind the interorbital constriction. The interorbital region is flat and the braincase is smooth. Skull is rather low and slightly convex when viewed in profile. Incisive foramina are short and lateral pits at the end of the palate are deep. Enamel pattern of M^3 varies little, having 4 (rarely 5) inner and 3 outer salient angles; BR4 is absent or obtuse. M_1 has 3 (rarely 4) outer and 4–5 inner re-entrant angles. Triangle T5 is closed; AC is of simple shape and broadly confluent with dental fields T6–7; BR4 is obtuse or absent and LR5 is frequently shallow (Figure 216a,b). Baculum shows no peculiarities; the proximal bone is 2.81 mm long and 1.53 mm wide at the base. Length of medial digit is 1.00 mm and of lateral digit is 0.60 mm (Aksenova 1980). Sperm head is semi-oval with conical acrosome situated on the apex (Malygin 1983). Karyotype: 2n=50, NF=60; X is large metacentric and Y is moderately large acrocentric (Orlov et al. 1978, Radjabli et al. 1984).

Variation and subspecies. Monotypic.

Alexandromys alpinus Lissovsky, Yatsentyuk, Petrova & Abramson, 2017 – Khangai Grass Vole

Alexandromys mongolicus alpinus Lissovsky, Yatsentyuk, Petrova & Abramson, 2017:10 (online edition; cf.

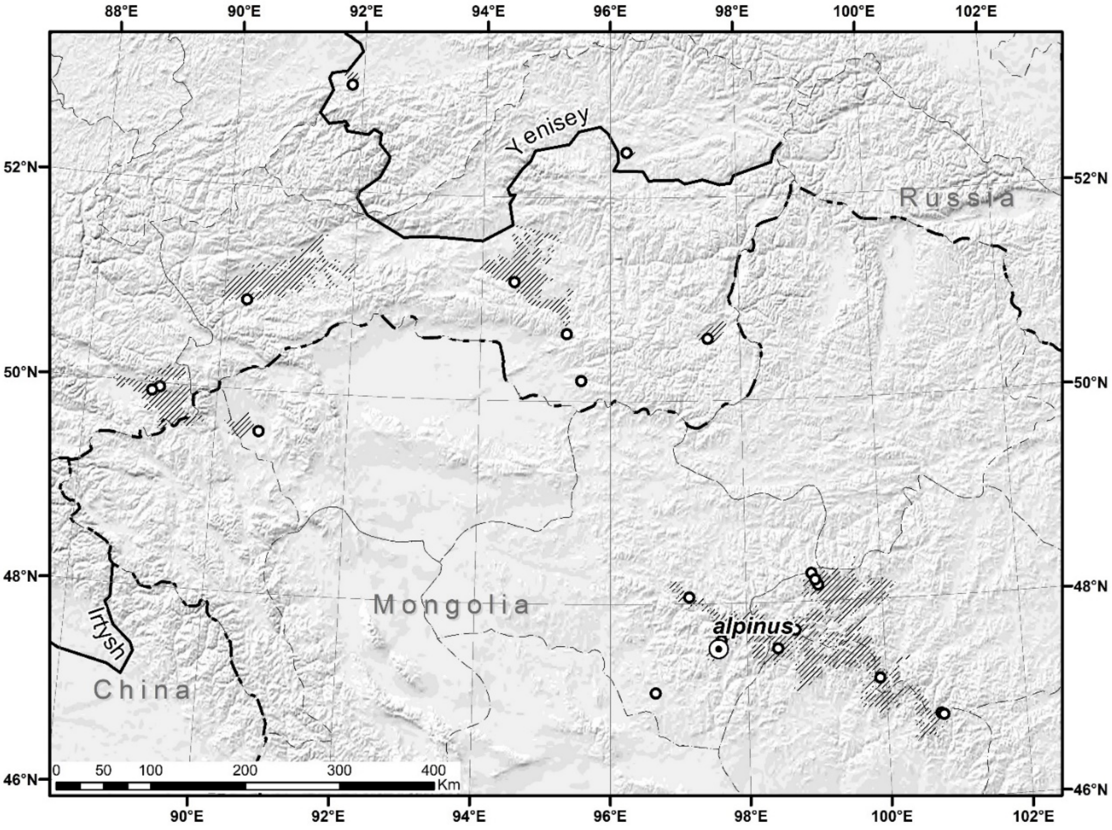


Figure 217: Distributional range of the Khangai grass vole *Alexandromys alpinus*.

Lissovsky 2018a). Type locality: "Mongolia, Khangai Mts, Bogdoin-Gol River, south foot of the Otkhon-Tengri (Otgontenger) Mt, approximately 47.68°N, 97.26°E" (Appendix S1 in the Supplementary information).

Taxonomy. Bannikova et al. (2019) elevated *alpinus* to a species in its own right. Possibly a sister species to *middendorffii*.

Distribution. (Figure 217). Range encompasses an estimated 23,000 km^2 in the Sayan Mts. (centred in Tuva) as far west as the Kosh-Agachsky District (Altai Republic; both Russia), and the Khangai Range in west-central Mongolia. Principal habitats are humid high-mountain grasslands and alpine tundra (Schvetsov et al. 1981) at 455–2,875 m a.s.l.

Characteristics. Similar to *mongolicus* but smaller and with a proportionally shorter tail (TL/H&B=0.18–0.27). Dimensions: BWt=16–27.3 g, H&B=88–125 mm, TL=21–29 mm, HF=13–15.5 mm, EL=9–14 mm, CbL=23.1–26.5 mm, ZgW=13.2–14.7 mm, MxT=5.3–6.6 mm. The tail is distinctly bi-coloured (blackish-brown above, silvery below), densely clothed with hair and with 5–8 mm long terminal pencil. Pelage is like in *mongolicus*, 7–9 mm long (sparse longer hairs up to 9–11.5 mm) but lighter on average. Back is frequently a clear buffy tint and never dark brown; the grizzled effect of light-coloured hair tips is less obvious than in *mongolicus*. Belly is grey, demarcation on flanks is faded. Skull like in *mongolicus* (ZgW/CbL=0.54–0.59); sagittal crest is more extensive, starting in the mid-orbital constriction, extending posteriorly until the parietals. Interparietal bone is squarish (lingulate in *mongolicus*). Mandible is deeper across the ramus; alveolar processus blunt and weak (Figure 215). Molars are essentially as in *mongolicus* (Figure 216c,d), except that M_1 has the BR4 present in >80% of individuals (in *mongolicus*, the proportion is <24%). Karyotype is indistinguishable from *mongolicus*: 2n=50, NF=60 (Yatsenko et al. 1980, Radjabli et al. 1984).

Subspecies. Monotypic.

Alexandromys middendorffii (Polyakov, 1881) – Middendorf's Grass Vole

Taxonomy and nomenclature. As late as the 1990s, the majority of authors regarded *hyperboreus* and *middendorffii* as distinct species, reportedly partially sympatric between the Lena and Kolyma Rivers (Tavrovskiy et al. 1971). The view that *hyperboreus* and *middendorffii* are conspecific is a newer assertion proposed by Pokrovskiy et al. (1975) and Yudin et al. (1976). Supporting evidence was provided by morphology and cross-breeding trials, karyology (Meyer et al. 1996) and nucleotide sequences (Bannikova et al. 2010).

Distribution (Figure 218). Middendorf's grass vole was long believed to be restricted to the Arctic Circle (cf. Map 60 in Kuznetzov 1944) and was classified as a member of sub-arctic (Shvarts & Pyastolova 1971) or polar fauna (Dobrinskiy & Sosin 1981). Subsequent records extended the range across boreal Russia to an estimated surface area of 1,568,400 km^2. The distribution is sporadic and the animal is uncommon (Kostenko 2000). The majority of records come from the Frigid Zone (i.e. to the north of the Arctic Circle) between the Kanin Peninsula (Nenetskiy Autonomous Okrug) and the head of the Manya River (Khanty-Mansiyskiy Autonomous Okrug) in the west, and the Sea of Okhotsk, Koryak Uplands, and Chukotka in the east. In central Siberia the localities are few and widely scattered in the Provinces of Buryatiya, Irkutsk, Khabarovsk, Krasnoyarsk, and southern Sakha, reaching Lake Baikal in the south. This vole is known only from the Russian Federation. Principal habitats in the Arctic zone are moist tundra, bogs, and dwarf birch shrubs; further south in the boreal zone Middendorf's vole occupies wet meadows in the flooding river valleys and inside broad-leaf woodland. The vole avoids flooded depressions which are the habitat of *A. oeconomus* (Andreev et al. 2006) and dry uplands occupied by *Stenocranius gregalis* (Shvarts & Pyastolova 1971). Altitudinal range is from sea level to 2,060 m a.s.l.

Description (Figure 202c). A moderately large vole with a short tail (TL/H&B=0.18–0-33). Hair is soft and dense, 8.5–12 mm long in the summer pelage (sparse protruding hairs up to 11–15 mm); winter hair is longer measuring up to 15 mm (protruding hairs up to 20 mm). Ears only slightly overtop the fur; there are 5 plantar pads. Tail is densely hairy and the underlying annulation is not visible; terminal pencil is long (11–13.5 mm). Colour varies individually and among subspecies. Back is of various shades of brown, flanks are lighter and belly is usually grey (see under subspecies); demarcation on the flanks is distinct. The tail is sharply bi-coloured, blackish-brown above, whitish-silvery below. The ears and paws are of various shades of grey. Cranially, *middendorffii* is similar to *mongolicus* or *shantaricus* (Figure 219); zygomatic arches are moderately expanded (ZgW/CbL=0.54–0.60). Interorbital crest is low and bifurcates behind the naso-frontal suture at the anterior end and before the fronto-parietal suture on the posterior side; the space inside the anterior fork of the diverging ridges is usually slightly depressed. Dental pattern is highly variable among individuals and even varies in the same animal; e.g. Bobretsov et al. (2011) found M^3 to be asymmetrical in 43% of voles from the Urals. This tooth has 4 (rarely 3 or 5) lingual and 4 (rarely 5) buccal re-entrant angles. M_1 normally has 5 lingual and 4 buccal re-entrant angles; LR5 is frequently deep (Figure 220a,b). Baculum: the proximal bone is long (=3.40 mm, basal width=1.66 mm); distal digits are characteristically short measuring 0.96 mm (central digit) and 0.52 mm (lateral digits; Aksenova 1980). Sperm head (length×width=9.03×5.92 µm) is semi-oval with the acrosome on the top of the apex (Aksenova 1978). Karyotype: 2n=50, NF=54; the X chromosome is large and bi-armed, the Y is small acrocentric or bi-armed (Gileva et al. 1979).

Variation and subspecies. Three subspecies are usually distinguished (e.g. Gromov Polyakov 1977, Shenbrot & Krasnov 2005); they were tentatively retrieved in a multivariate analysis of cranial

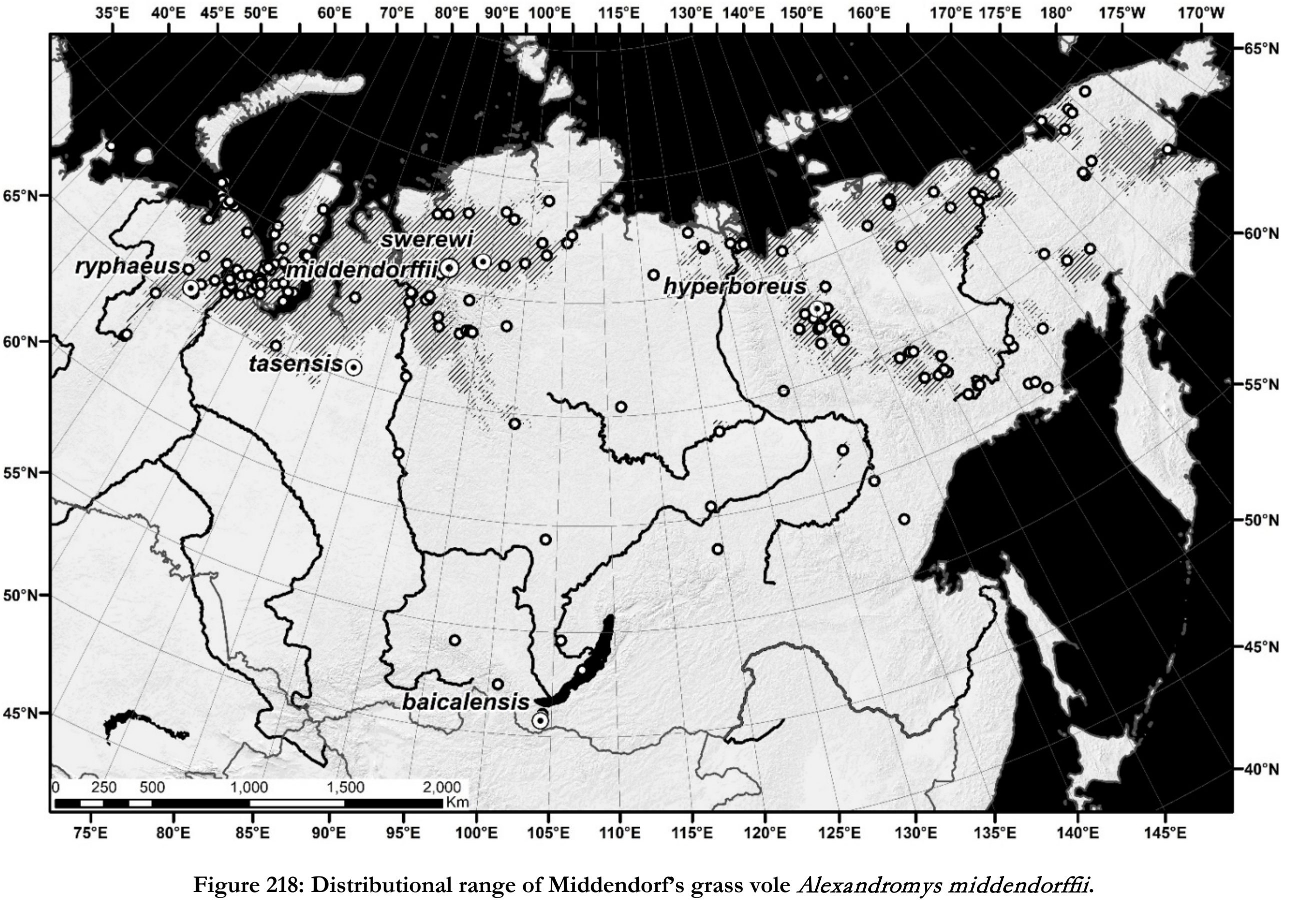


Figure 218: Distributional range of Middendorf's grass vole ***Alexandromys middendorffii*.**

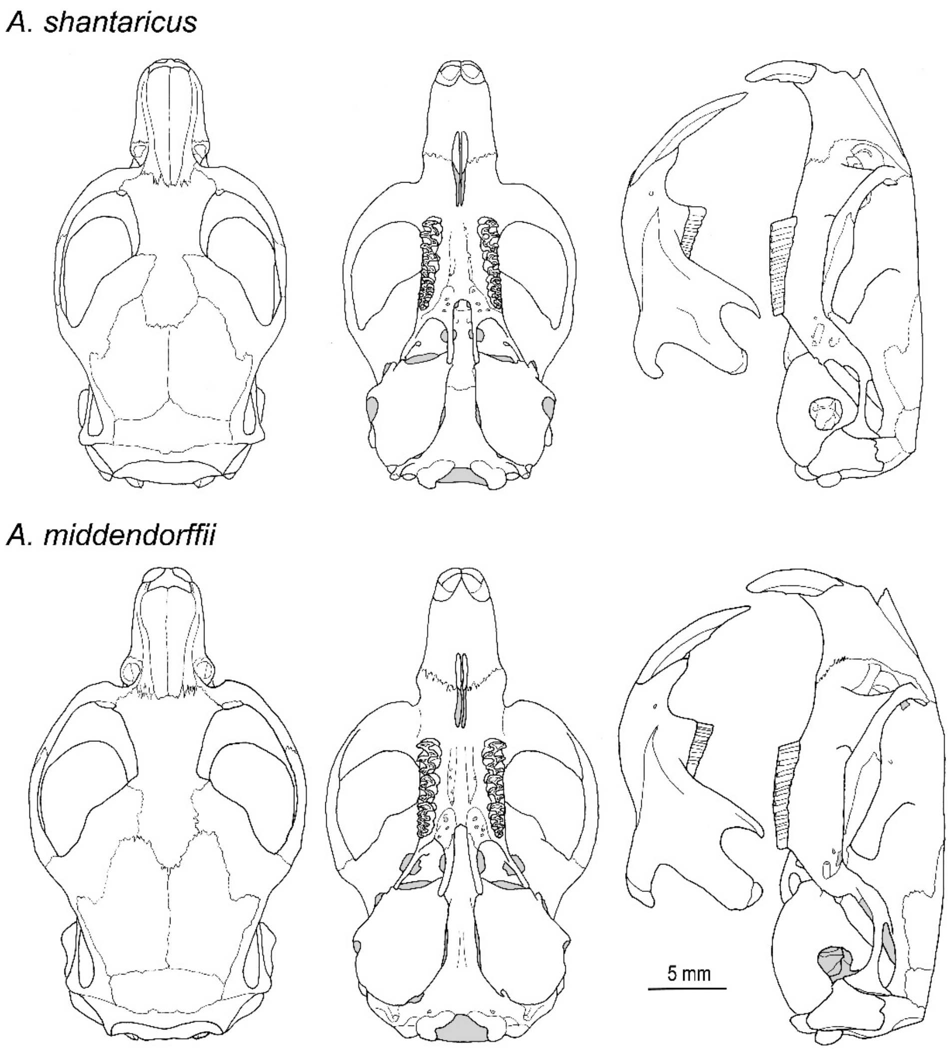


Figure 219: Skull and mandible of *Alexandromys shantaricus gromovi* (Aleutskoe Lake, Khabarovsk Krai; top) and *A. middendorffii* (Tomtor, Verkhoyanskiy ulus, Sakha; bottom).

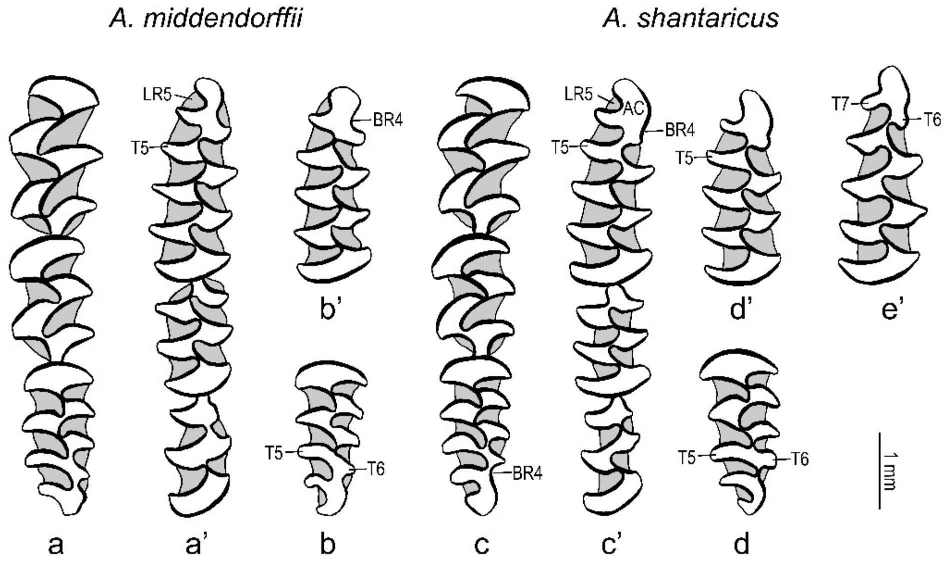


Figure 220: Molar pattern in *Alexandromys middendorffii* and *A. shantaricus*. *A. middendorffii*: upper (a) and lower row (a’–Norilsk, Taymyr, Russia); isolated M^3 (b) and M_1 (b’–ssp. *hyperboreus*). *M. shantaricus gromovi*: upper (c) and lower row (c’) and isolated M_1 (e'); *A. shantaricus shantaricus*: isolated M^3 (d) and M_1 (d’).

measurements (Lissovsky et al. 2010). Voles living in Taymyr, Yakutia and Chukotka presumably diverged 45–54 kya (Bannikova et al. 2010).

Alexandromys middendorffii middendorffii (Poljakov, 1881)

Arvicola Middendorffii Polyakov, 1881:70. Pavlinov & Rossolimo (1987:201) subsequently restricted the type locality to "Krasnoyarsk Krai, Taymir Autonomous Oblast, Dudypta River", Russia.

Synonyms. *Microtus middendorffi tasensis* Skalon, 1935; *Microtus hyperboreus swerevi* Skalon, 1935; *Microtus arvalis baicalensis* Fetisov, 1941.

Distribution. Western and Central Siberia, from the Ob' Delta and Taz Gulf in the west to Khatanga Bay in the east; possibly includes a population from Baydaratskaya Bay between the Urals and Yamal (cf. Lissovsky et al. 2010). Taxonomic position of voles from eastern Sayan Mts, and the shores of Lake Baikal, which in the past were ascribed to the nominal subspecies or to *baicalensis* is not known with certainty.

Characteristics. The largest subspecies: BWt=34–84 g, H&B=100–147 mm, TL=23–40 mm, HF=15.2–21.0 mm, EL=8–15 mm, CbL=26.3–31.4 mm, ZgW=15.0–18.1 mm, MxT=6.0–7.5 mm. Dorsal fur is clear brown, in some cases grizzled buff, flanks are either buffy or grey-brown, the underside is whitish-grey to dark-grey, demarcation is fairly distinct. Paws are grey. M^3 has 4 salient angles on each side in ~80% of cases (Bobretsov et al. 2011).

Alexandromys middendorffii ryphaeus (Heptner, 1948)

Microtus middendorffi ryphaeus Heptner, 1948:710. A substitute name for *Microtus middendorffii* natio *uralensis* Vinogradov & Argyropulo, 1941, a homonym of *uralensis* Polyakov (see below).

Synonyms. *Microtus middendorffi* natio *uralensis* Skalon, 1935 [available from Vinogradov & Argyropulo 1941; preoccupied by *uralensis* Polyakov, 1881].

Taxonomy. Subspecies *ryphaes* is in a sister position against the remaining subspecies combined (Lissovsky et al. 2010). Kuznetzov (1944) listed *swerevi* as part of *hyperboreus*.

Distribution. Shores of the Barents and Kara Seas between the Kanin and the Yamal peninsulas and the northern Ural Mts. (Nenets Autonomous District and western parts of Yamalo-Nenets and Khanty-Mansi Autonomous Districts).

Characteristics. The smallest subspecies: BWt=27–50 g, H&B=105–137 mm, TL=22–41 mm, HF=15.5–20.5 mm, EL=9–17 mm, CbL=25.7–28.9 mm, ZgW=15.2–16.7 mm, MxT=6.2–6.8 mm. Back is light, above ocher-brownish and shaded russet; snout is sayal-brown, cheeks and the post-auricular region are yellowish. Flanks are light buffy or yellowish, the demarcation is fairly distinct; underside is light whitish-grey, clouded by slate hair bases. Paws are whitish-grey. M^3 has 4 salient angles on each side in 56 % of cases; 32 % of molars have 3–4 lingual and 3 buccal salient angles. M_1 has 5 inner salient angles in 69 % of cases and 6 angles in 30% (Bobretsov et al. 2011).

Alexandromys middendorffii hyperboreus (Vinogradov, 1933)

Microtus hyperboreus Vinogradov, 1933:72. Emended description published in Vinogradov (1935:82–83). Type locality: "Verkhoyansk ridge and several other spots in the Verkhoyansk District"; subsequently determined by the lectotype (Ognev 1950:243) to "R[iver] Adycha, near the village of Adychinska [Adychenskaya], Verkhoyansk District", Sakha, Russia.

Distribution. Eastern Siberia: the Lena River (east of 125° east longitude), Omoloy, Yana, Alazeya, Khroma, Indigirka, Kolyma, Palyavaam, Keveem, Kuvet and Anadyr River Basins in Yakutia, Magadan Oblast and Chukotka.

Characteristics. Size intermediate between the nominal subspecies and *ryphaeus*: BWt=30–70 g, H&B=102–145 mm, TL=23–36 mm, HF=16.5–20 mm, EL=11–15 mm, CbL=24.5–31.6 mm, ZgW=13.7–

18.0 mm, MxT=6.3–7.5 mm. Pelage the darkest, dorsal side varies from clear brown with a buffy tint and a yellowish post-auricular tuft, to dark brown, or even a dull blackish-brown. Flanks are buffy-brown to brown-grey, the underside is whitish-grey to slate-grey. Paws are grey to dull-grey. M^3 has 4 salient angles on each side (Figure 220b) in ~80% of cases (Bobretsov et al. 2011).

Alexandromys shantaricus (Ognev 1929) – Gromov's Grass Vole

Taxonomy. The *shantaricus* and *gromovi* were long regarded as belonging to two different polytypic species of grass vole: the former to *oeconomus* and the latter to *maximowiczii*. Kartavtseva et al. (2008) endorsed *gromovi* as a species in its own right on the basis of karyological evidence which was supported in subsequent studies (Sheremetyeva et al.2009). Finally, Dokuchaev & Sheremetyeva (2018) demonstrated the paraphyly of *gromovi* with respect to *shantaricus* and concluded that these taxa are conspecific.

Distribution (Figure 221). Range (=26,495 km^2) is in 2 clusters of fragments in the Sea of Okhotsk (eastern Russia). One isolate is along the Yama River (Magadan Oblast) and the other stretches from Ayan to Ulbanskiy Bay (Province of Khabarovsk Krai), encompasses Shantar Island and penetrates inland till Neryungrinskiy District (Sakha–Yalutia). Gromov's vole occupies low-lying wet meadows with sedge, cotton-grass and grasses in river valleys and along the seashore. Altitudinal range is from sea level up to 1,080 m a.s.l.

Description. A small and short-tailed (TL/H&N=0.24–0.33) grass vole. There are 6 plantar pads (Ognev 1929); tail is densely clad by hairs, terminal pencil measures 3 mm (summer) to 5–8 mm (winter). Ears slightly overtop the fur. Summer fur is 7–8.5 mm long (protruding hairs 9–12 mm) and somewhat shaggy; winter hair is soft and dense (length=9–11.5 mm, protruding hairs=11–14 mm). Colouration differs between populations (see under subspecies) but the snout is always buffy. The tail is sharply bi-coloured, blackish above, greyish-white below, ears and paws are grey. Skull is rather narrow (ZgW/CbL=0.51– 0.58) and shallow (Figure 219). Enamel pattern is complex (Figure 220c-e'): M_1 with 5 (rarely 4) inner and 3–4 outer re-entrant angles; T5 is either isolated or confluent to the AC; BR4 is usually obtuse and LR5 is normally deep. M^3 has 4 inner and 3–4 outer re-entrant angles; BR4 is feeble (Dokuchaev 2014); triangles T5–T6 are typically confluent (Bannikova et al. 2010). Karyotype: 2n=44,

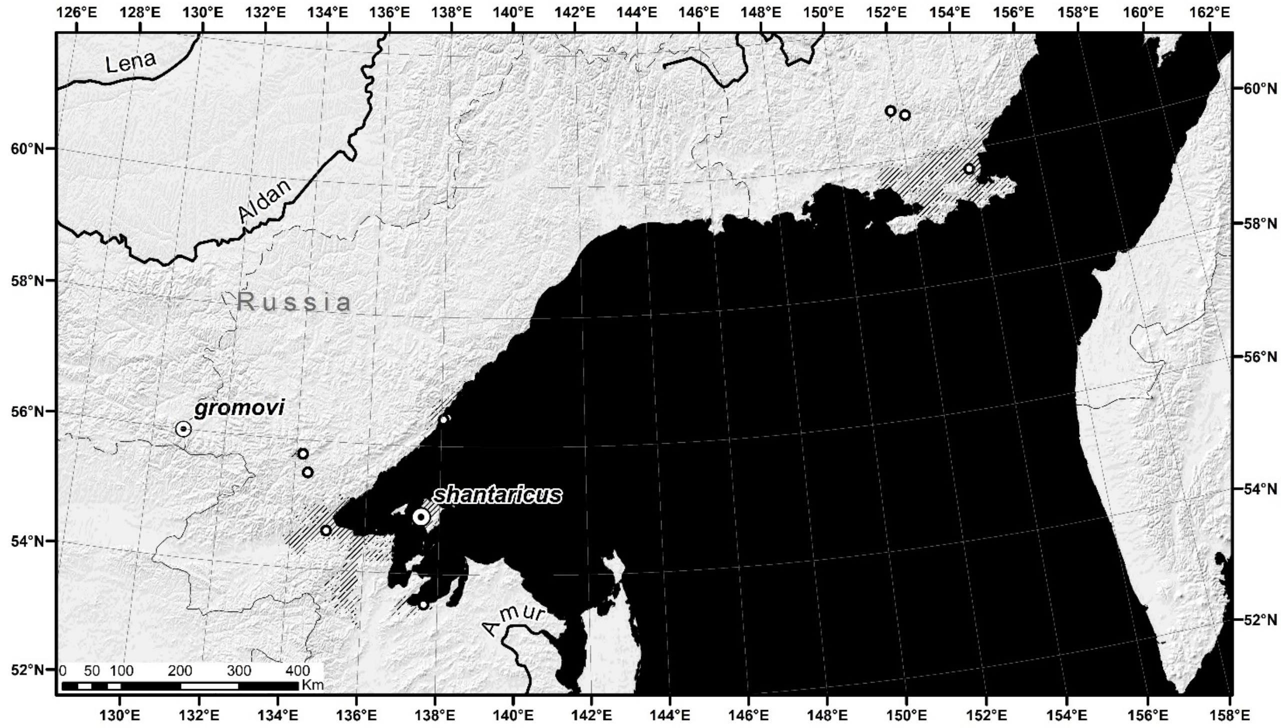


Figure 221: Distributional range of Gromov's grass vole *Alexandromys shantaricus*.

NF=60; there are 16 pairs of bi-armed and 28 pairs of acrocentric chromosomes; both sex chromosomes are acrocentric (Vorontsov et al. 1988, Kartavtseva et al. 2008, Sheremetyva et al. 2009).

Variation and subspecies. We classify *shantaricus* as a distinct insular subspecies.

Alexandromys shantaricus shantaricus Ognev, 1929

Microtus oeconomus shantaricus Ognev, 1929:22. Type locality: "estuary of the River Yakshino, Boshoy Shantar [Great Shantar Island]", Sea of Okhotsk, Russian Federation.

Distribution. Endemic to Bolshoy Shantar Island.

Characteristics. Larger: BWt=40 g, H&B=107–125 mm, TL=28–35 mm, HF=16.5–19 mm, EL=10.7–12.3 mm, CbL=27.1–29.7 mm, ZgW=15.0–17.2 mm, MxT=6.5–7.2 mm. Pelage is lighter with fawn-brown snout, front and back; flanks are heavily clouded buffy and the demarcation is rather sharp; belly is light-grey.

Alexandromys shantaricus gromovi Vorontsov, Boeskorov, Lyapunova & Revin, 1988

Microtus maximowiczii gromovi Vorontsov, Boeskorov, Lyapunova & Revin, 1988:212. Type locality: "east coast of Lake Bol'shoe Toko, Basin of the Aldan River, ridge of Tokinskiy Stanovik, the border between Yakutsk ASSR [Republic of Sakha] (Neryungrinsk rayon) and Khabarovsk Krai … 900 m a.s.l.", Russia.

Distribution. The mainland portion of the species range.

Characteristics (Figure 202b). Smaller: BWt=37–47 g, H&B=89–115 mm, TL=22–32 mm, HF=15–18 mm, EL=10–14 mm, CbL=22.8–26.8 mm, ZgW=12.6–14.7 mm, MxT=5.4–7.1 mm. Pelage is darker, clear brown and grizzled with buffy or rusty hair tips; the sides are buffier and the demarcation line is distinct; underside is dull grey with light-silver patches. In some individuals the eyes are encircled by light-grey hairs which extend in a narrow stripe towards the ear base.

SUBGENUS: *Oecomicrotus* Rabeder, 1981

Oecomicrotus Rabeder, 1981:300. Type species: *Microtus oeconomus* (Pallas, 1778).

Synonyms. *Paludicola* J. H. Blasius, 1857 [antedated by Wagler (1830) for Lissamphibia and Hodgson (1837) for Aves]; *Pallasiinus* Kretzoi, 1964 [unavailable name].

Taxonomy. This subgenus, used here for *oeconomus* and *limnophilus*, is widely known as *Pallasiinus* which, however, is an unavailable name.

Distribution. Holarctic.

Characteristics. Small to moderately large grass voles with 6 plantar pads and 8 nipples. Baculum has distal trident osseous. M1: antero-lingual triangle T5 is isolated from the anterior cap; antero-labial salient angle BS4 is obtuse or entirely absent. Karyotype: 2n=30 or 38.

Alexandromys oeconomus (Pallas, 1776) –Tundra Grass Vole, Root Vole

Mus *oeconomus* Pallas, 1776:693. Type locality: "omnem Sibiriam etiamin borealibus, et ad orientem uſque in Kamtſchatkam", subsequently restricted to "Ischim Valley" (Ognev 1944a:180, Kuznetzov 1944:352), in Tyumen Oblast, western Siberia, Russia.

Synonyms. *[Mus oeconomus]* varietas *kamtschatica* Pallas, 1779; *Arvicola ratticeps* Keyserling & J. H. Blasius, 1841; *Arvicola arenicola* Selys, 1841; *[Lemmus] medius* Nilsson, 1844; *Arvicola kamtschatica* Polyakov, 1881 [antedated by *kamtschatica* Pallas, 1779]; *Arv[icola] oeconomus* var. *uralensis* Polyakov, 1881; *Arv[icola] (Microtus) ratticeps* var. *Stimmingi* Nehring, 1899; *Microtus tshuktshorum* Miller, 1899; *Microtus oeconomus* var. *daurica* Kashchenko, 1910; *Microtus koreni* G. M. Allen, 1914; *Microtus uchidæ* Kuroda, 1924; *Microtus ratticeps Méhelyi* Éhik, 1928; *Microtus oeconomus suntaricus* Dukelski, 1928; *Microtis* [*sic*] *uchidai* Kishida, 1930: *Microtus oeconomus hahlovi* Skalon, 1935;

Microtus oeconomus kjusjurensis Kolyuschev, 1935; *Microtus oeconomus naumovi* Stroganov, 1936; *Microtus oeconomus anikini* Egorin, 1939; *Microtus ratticeps petshorae* Ognev, 1944; *Microtus ratticeps altaicus* Ognev, 1944; *Microtus ratticeps montium-caelestinum* Ognev, 1944; *Microtus oeconomus finmarchicus* Siivonen, 1967; *M[icrotus] o [economus] karaginensis* Kostenko, 1984 [nomen nudum]; *Microtus oeconomus karaginensis* Kostenko & Allenova, 1989; *Microtus oeconomus kharanurensis* Courant, Brunet-Lecomte, Volobouev et al., 1999. For Nearctic synonyms see Hall (1981).

Taxonomy and nomenclature. From the mid-19th till the mid-20th century *oeconomus* was used interchangibly with *ratticeps*; Ellerman & Morrison-Scott (1951) favoured the former name which ensured its wide acceptance. The tundra grass vole was frequently classified apart from other grass voles either into subgenus *Pallasiinus* or the *oeconomus* species group. *Pallasiinus* infrequently also contained *kikuchii, limnophilus* and/or *montebelli*, depending on the author. The close relationship of *oeconomus* and *limnophilus* was stipulated in Steppan & Schenk (2017). Vorontsov et al (1986) suggested that the karyotype of *oeconomus* can be inferred from that of extant *limnophilus*.

Distribution (Figure 222). Holarctic temperate, boreal and polar zones. In the Palearctic, *oeconomus* ranges from the lower Rhine (the Netherlands) and mid-Danube (eastern Austria, north-western Hungary and south-western Slovakia) in the west to Kamchatka, Chukotka and the Sea of Okhotsk in the east. It is also present in Alaska and northern Canada (Northwest Territories, British Columbia, Nunavut and Yukon). The time of trans-Beringian colonisation is disputed. The fossil history of *oeconomus* in the New World dates back to the Late Illinoian (corresponding to Saalian, i.e. >130 kya) (MacDonald & Cook 2009) although molecular dating suggests the tundra grass vole to be a later coloniser (Lance & Cook 1998). The entire range covers 12,772,000 km². The westernmost Palaearctic records in the Netherlands, Austria, Hungary, Slovakia, and south-western Norway are geographic isolates. The range is mostly contiguous in north-eastern Germany, Poland, Belarus, Latvia, northern Ukraine, eastern Fennoscandia, across Russia, northern Kazakhstan and northern Mongolia. The 50th parallel, which roughly sets the southern border, is transgressed in eastern Kazakhstan (Semyrechensk), north-eastern Xinjiang (China) and Mongolia; the most exposed records are on the Tien Shan. The northern border tentatively follows the shores of the Arctic Ocean, although there are also

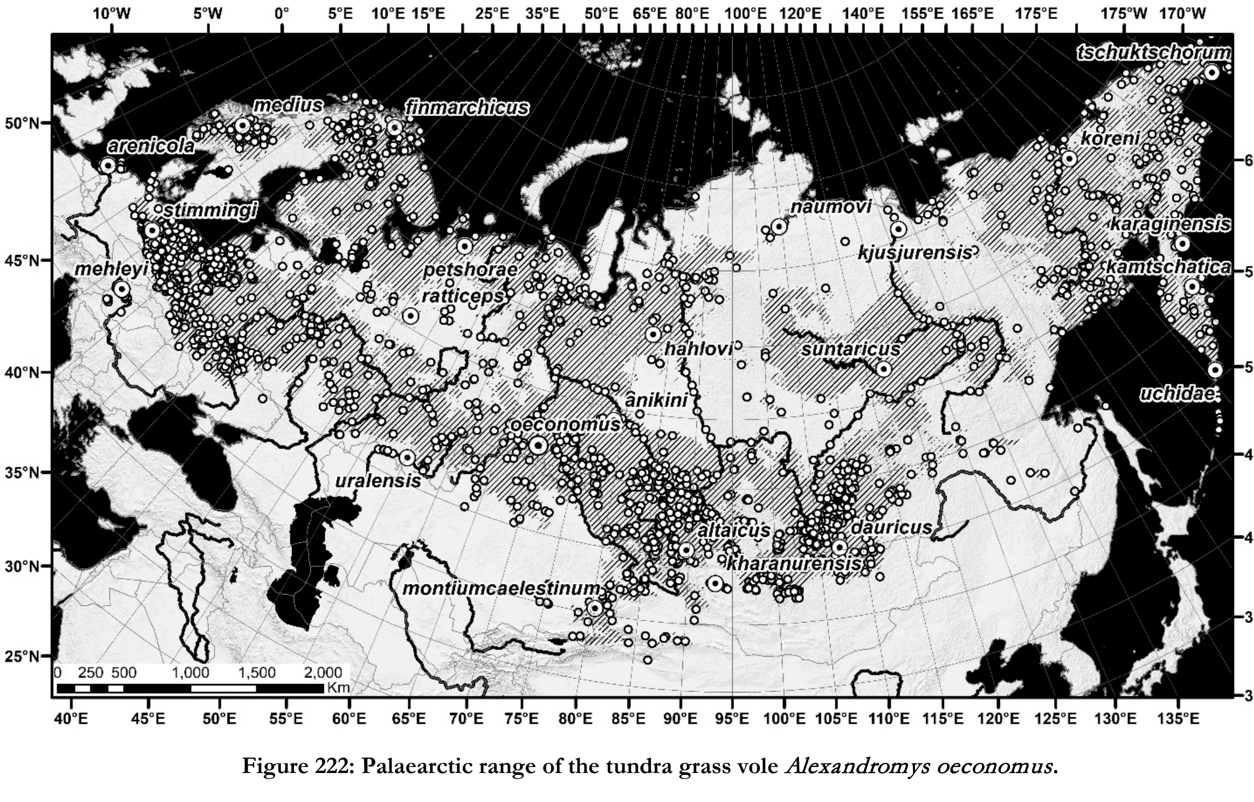


Figure 222: Palaearctic range of the tundra grass vole *Alexandromys oeconomus*.

vast areas where no root voles are present, i.e. on the northern parts of the Yamal, Gyda and Taymyr Peninsulas, and on the majority of the coast of the Laptev Sea. Range expansion since the 1990s has been documented in Lithuania (Balčiauskas et al. 2010) and in the Saratov district in European Russia (Shlyakhtin et al. 2009). The range was more extensive in the Late Pleistocene and Early Holocene, encompassing among others Central and Western Europe as far south as central Italy and northern Iberia (Laar 2018). Present on the islands: Texel, Vlieland and Zeeland off the Atlantic coast of the Netherlands (Laar 2018), Baltic islands offshore Germany (Rügen, Riehm, Bock), in the gulf of Bothnia off the Finnish coast, the *Vesterålen* archipelago in the Norwegian Sea (Niethammer & Krapp 1982), in the East Siberian Sea (Ayon), Bering Sea (Yittingran, Karaginsky, Verkhoturov) and in the North Kurils archipelago (Shumshu, Atlasov (=Alaid), and Paramushir). In 1915 translocated from Shumshu and Paramushir to Ushishir; from there it was transferred to other Central Kuril islands in 1917–1918 (Bobrov et al. 2008); now present on Onekotan, Kharimkotan, Shiashkotan, Matua, Rasshua, Ketoy, Ushishir (=Ryponkicha), and Simushir. Occupies Bol'shoy Toynik and Ol'khon islands in Lake Baikal, and smaller islands in some lakes and rivers (e.g. Volga, Ob'). Voronov's (1974) report for northern Sakhalin was not confirmed (Kostenko 2000, Burkovskiy 2005). The root vole is present on the islands offshore Alaska, including St. Lawrence and several of the Aleutians islands (MacDonald & Cook 2009). Inhabitant of marshy and damp environments with dense and lush vegetation cover, frequently around lakes, ponds and riverbanks: reedbeds, swamps, bogs, marshes, saline sedge meadows, and flooded river valleys with willow shrubbery. In steppe and desert landscape strictly tied to the proximity of water. Following river valleys, the tundra grass vole penetrates deep into the tundra belt, although it avoids open lichen tundra. Occasionally present on mowed pastures, in sparse woodland and in clearings inside forests. At high elevations (up to 2,500 m) occupies spruce forests, shrubby habitats and alpine meadows. In the north *A. oeconomus* is synanthropic (Chernyavskiy 1984, Balčiauskas et al. 2010).

Description (Figure 202f). A grass vole of average size: BWt=20–90 g, H&B=97–161 mm, TL=23–74 mm, HF=16–23 mm, EL=11–15.5 mm, CbL=23.9–31.2 mm, ZgW=13.1–18.5 mm, MxT=5.8–8.2 mm. Tail is moderately long (TL/H&B=0.37–0.57) and sparsely clad with hairs which do not conceal the annulation; terminal pencil is 4–10 mm long. Males can be up to 45% heavier than females. There are 5 large palmar pads; 6 plantar pads (rarely 5), small, of similar size and densely packed (Figure 204c). Fur is 7.5–12.5 mm long on the midback; scattered longer hairs measure 10–18 mm. Colour varies individually and between regions. Back is normally brown to dark brown and grizzled by black hair tips. Black tints frequently dominate along the spine, on the nape and front, and occasionally spread laterally. Lighter populations have ochre-brownish back which may be shaded russet; the rump is usually brighter than the nape and front. Flanks are lighter with more buff suffusion; demarcation along the flanks is distinct. Belly is of various shades of grey from light grey with silver or cream grizzling to dull grey; a buffy or brown tint is quite common. Tail is nearly uniformly blackish in dark voles to distinctly bi-coloured (brown above, whitish or grey below) in lighter ones. Feet vary from light brownish-grey to blackish grey; ears are grey to blackish. Skull shows no peculiarities (Figure 223); zygomatic arches are narrow to moderately expanded (ZgW/CbL=0.50–0.57) and the braincase is stretched out. The molar pattern is relatively stable (Figure 224). M_1 has 3 outer re-entrant angles; T5 is usually confluent with AC (in ~95% of voles from Central Europe). M^3 has 3–4 outer and 4 (rarely 5) inner salient angles (cf. Bol'shakov et al. 1980). The proximal baculum is 2.50–3.95 mm long and 1.10–2.45 mm wide across basal expansion. Medial distal baculum measures 0.58–1.30 mm, therefore accounting for $^1/_3$ the length of the proximal baculum; lateral distal digits (length=0.55–1.20 mm) rarely do not ossify. The base of the stalk almost never has a deep median notch (Ognev 1950, Aksenova 1980). Sperm head (length×width=7.00×3.57 μm) is falciform (Aksenova 1978).

Karyotype: 2n=30, NF_a=56. All autosomes are bi-armed; X is medium submetacentric and Y is small acrocentric (Zima & Král 1984, Frisman et al. 2003). Chromosomal polymorphism (2n=31, 32) due to centromeric fission was reported from Sweden, Norway (Fredga et al. 1986), north-western Russia (Baskevich et al. 2016b), and western Siberia (Vorontsov et al 1986).

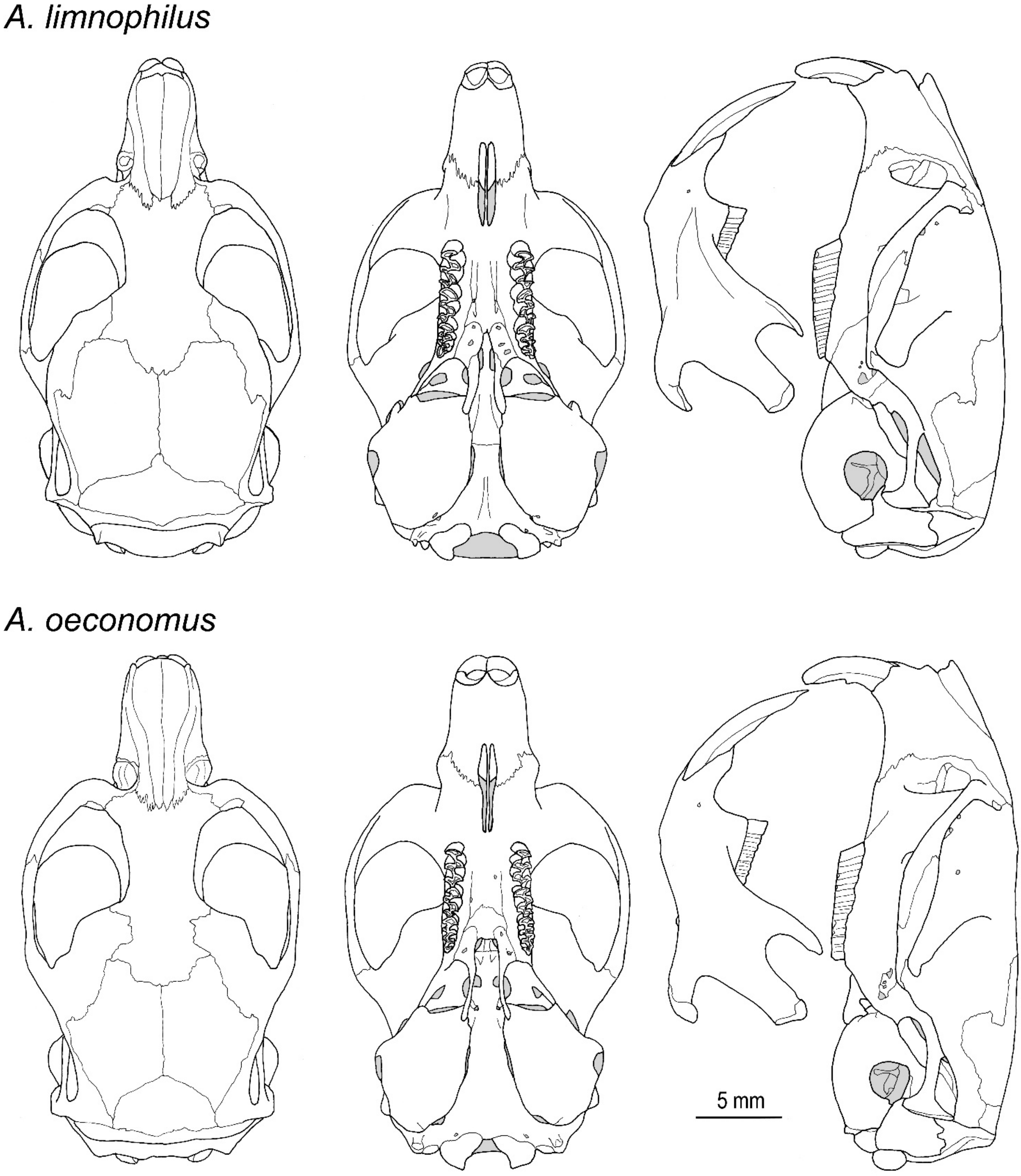


Figure 223: Skull and mandible of *Alexandromys limnophilus* (Taochow, Kansu, China; top) and *A. oeconomus* (Berdsk, Novosibirsk, Russia; bottom).

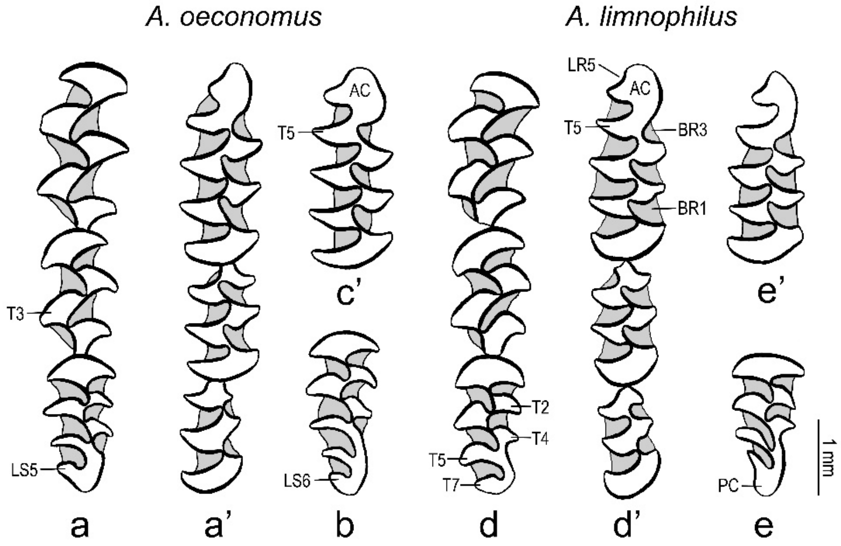


Figure 224: Molar pattern in *Alexandromys oeconomus* and *A. limnophilus*. *A. oeconomus*: upper (a) and lower row (a'–Jotunheimen, southern Norway); isolated M³ (b–Csomend-Taska, Hungary) and M₁ (c'–Wilsichow, Brandenburg, Germany). *A. limnophilus*: upper (d) and lower row (d'–Zaidam, Quinghai, China), and isolated M³ (e) and M₁ (e'–Tschortentan, Gansu, China).

Variation and subspecies. Variation in colour, size, molar pattern and molecular makeup was retrieved in many studies throughout the extensive range of the tundra grass vole. Cyt*b* haplotypes cluster into two major groups (European and Asiatic) separated by the Ural Mts. The European group is further structured into the Central European (western Scandinavia, Baltic region, Poland, Netherlands, Hungary, Slovakia, and Austria) and the Northern European lineage (eastern Fennoscandia, Belarus, and European Russia). The Asiatic lineage consists of the Central Asian lineage (the majority of Asian Russia) and the Beringian lineage (north-eastern Russia, Canada and Alaska) (Brunhoff et al. 2003) which meet on the Omolon River. Further substructuring was retrieved in each of these lineages.

A considerable number of subspecies have been recognised with little consensus among various authors. Compilations which covered the entire Palaearctic list 15–20 subspecies (Ellerman & Morrison-Scott 1951, Shenbrot & Krasnov 2005, Pardiñas et al. 2017). Kostenko (1989) failed to retrieve geographically meaningful clustering in eastern Siberia and the Far East.

The majority of populations and subspecies are dark brown. Blackish (fuscous) tint characterises populations in the west, eastern Siberia, Baikal and on the Tien Shan, while voles from Kamchatka and Chukotka are light (drab, cinnamon buff). In East Asia voles tend to be light along the coast, dark inland and intermediate in-between (Kostenko 1989). The pattern of morphometric variability of M³ and M₁ in various Asiatic populations showed little geographic association but correlated with environmental factors. There was not much concordance between the variations of the two molars (Pozdnyakov & Litvinov 1994).

Alexandromys limnophilus (Büchner, 1889) – Lacustrine Grass Vole

Taxonomy. Büchner (1889) compared *limnophilus* only with *M. tianschanicus* (=*Stenocranius gregalis*), hence its relationship to *oeconomus* remained unclear for a considerable time. Orlov et al. (1978) showed that *limnophilus* and *oeconomus* differ chromosomally, Sokolov & Orlov (1980) defined morphological differences distinguishing them, and Malygin et al. (1990) disclosed that they do not hybridise. While the status of *limnophilus* as a species in its own right is robustly supported, its phylogenetic relationships are less clear. In various molecular reconstructions, *limnophilus* emerged as a sister species to *fortis* (Bannikova et al. 2010) or to *oeconomus* (Steppan & Schenk 2017), or as a basal species in the *middendorffii* group (Lissovsky et al. 2018a). Its acoustics are distinct from both *oeconomus* and *middendorffii* (Rutovskaya 2020). Karyotypes of *limnophilus* and *oeconomus* are easily homologised (Orlov et al. 1978, Malygin et al. 1990).

Distribution (Figure 225). The range covers 415,020 km² in 2 major fragments, one in west-central China and the other in western Mongolia. The vicariance, however, might be a misconception due to sampling gaps (Sheftel et al. 2017). The bulk of the range is in the watershed of the upper Yellow River in Gansu, Qinghai, Shaanxi, and Sichuan, with marginal records in Nei Mongol and Ningxia (all in China). The Mongolian part of the range is in the mountain ranges of Mongol Altai and Govi Altai, in the Great Lakes Depression, the Valley of the Lakes, and in the deserts of Dzungarian Govi and Trans-Altai Govi. An earlier report for the Zaysan Depression, eastern Kazakhstan (Gromov & Polyakov 1977), is erroneous. As implied by its name the species frequents dense vegetation along the banks of rivers and lakes (Xu 2016) and is restricted to oases in a desert landscape. Altitudinal range is 480–4,270 m.

Characteristics. A small grass vole with a moderately long tail (TL/H&B=25–44). The tail is densely haired and the underlying annulation is barely visible; the terminal pencil is short (2–5.5 mm) and the hairs are frequently scarce. The ears protrude above the fur. There are 5 palmar and 6 plantar pads. Metacarpal pads are pronouncedly large (the medial pad is the largest) and touch one another medially (Figure 203c). Plantar pads are of comparable size; the medial interdigital pad is positioned posterior to the lateral interdigital pad, being at approximately the same level as the lateral metatarsal pad. Fur is soft, 7–9 mm long; the sparse protruding hairs measure up to 9–14 mm. The dorsal

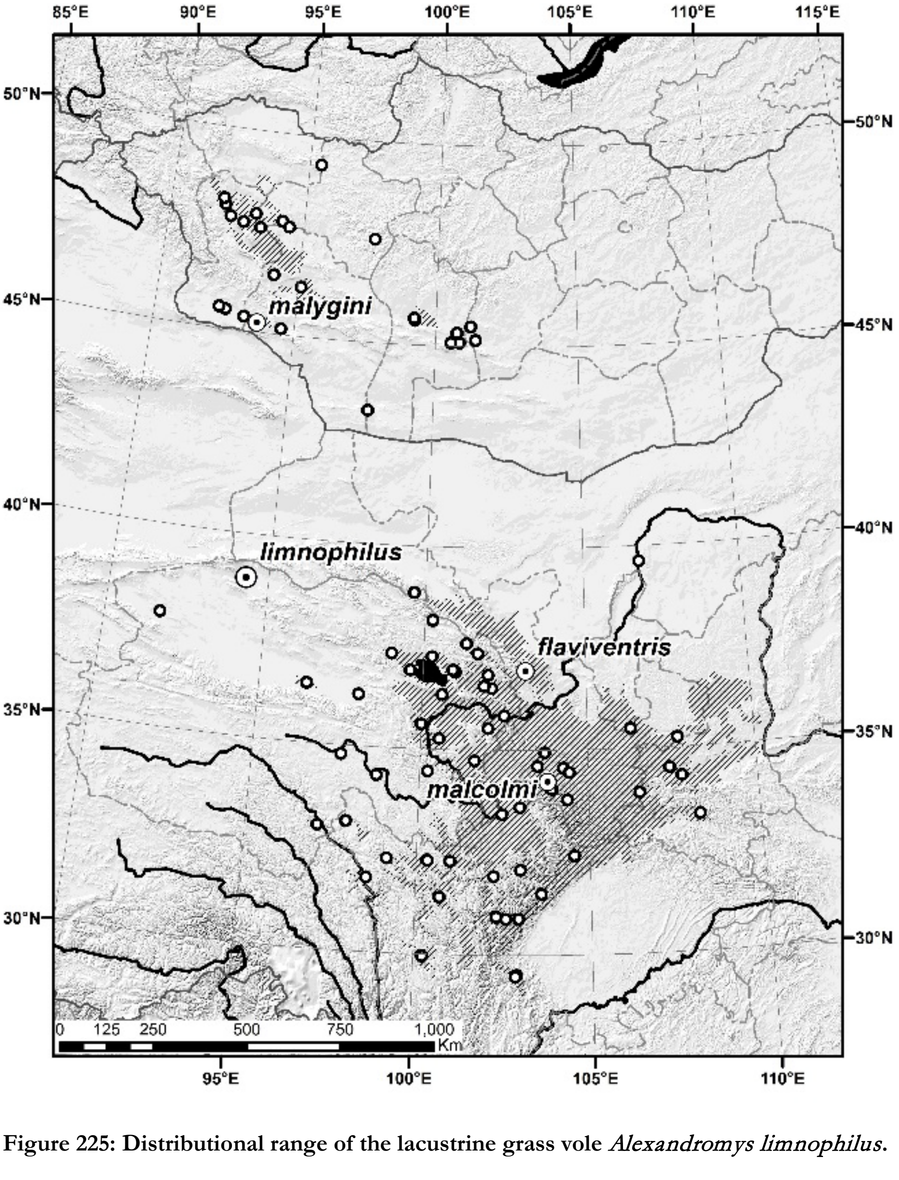


Figure 225: Distributional range of the lacustrine grass vole *Alexandromys limnophilus*.

side is usually light brown and grizzled buffy-grey; hairs in the auricular region are normally yellowish. Flanks are brighter and more buff; underside is whitish-grey, frequently with a light buffy tint. Paws are whitish grey, ears are grey and tail is sharply to indistinctly bi-coloured, grey to blackish-brown above and grey below. Baculum: the proximal bone (length=3.1–3.3 mm) has an extensive triangular base (width=1.65–1.8 mm). Distal baculum is osseous; the medial digit (length=0.9–1.1 mm, width=0.35–0.5 mm) is the same length as the lateral digit (0.3–0.5 mm; Liu et al. 2007).

The skull is well-built, comparatively narrow (ZgW/CbL=0.53–0.58) and rather deep. From the lateral view the angle at which the nasals slope downward is more conspicuous than in *oeconomus* (Figure 223). The sagittal crest is marked and long but low. Molar pattern is as in *oeconomus*, i.e. M_1 has T5 widely confluent with the AC; there are 3 buccal re-entrant angles. M^3: the buccal side has 2 triangles (T2 and T4); T4 narrowly opens into the PC which also encompasses the dental fields of T5 and T7 (Figure 224d-e). Karyotype: 2n=38, NF_a=54; there are 7 metacentric, 2 submetacentric, and 9 acrocentric pairs of autosomes; X is medium-sized bi-armed and Y is small acrocentric (Orlov et al. 1978; Malygin et al. 1990).

Variation and subspecies. Differences between subspecies were retrieved in a multivariate analysis of molars (Courant et al. 1999). Sheftel et al. (2017) stressed the low inter-subspecific *Cytb* distance (<2%).

Alexandromys limnophilus limnophilus (Büchner, 1889)

Microtus limnophilus Büchner, 1889:110+Plates XVII (Fig. 4) & XVIII (Figs. 11–13). Syntypes are from "Ganssy, Zaidam [Gansy, southern Zaidam]" and "Ssyrtyn, Zaidam [Syrtyn, north-western Zaidam]", Quinghai, China.

Synonyms. *Microtus limnophilus flaviventris* Satunin, 1903; *Microtus malcolmi* Thomas, 1911.

Characteristics. Smaller: BWt=26–35 g, H&B=100–120 mm, TL=29–49 mm, HF=14–18 mm, EL=12–16 mm, CbL=23.7–26.6 mm, ZgW=13–15 mm, MxT=5.7–6.6 mm. M_1 with more slender anteroconid complex; LR5 frequently present but shallow.

Distribution. China.

Alexandromys limnophilus malygini (Courant et al., 1999)

Microtus limnophilus malygini Courant, Brunet-Lecomte, Volobouev, Chaline, Quéré, Nadachowski, Montuire, Bao, Viriot, Rausch, Erbajeva, Shi, & Giraudoux, 1999:479. Type locality: "Stream [a spring of] Gun Tata Bulak, Dzhungar Gobi, Mongolia."

Characteristics. Larger: BWt=26–58 g, H&B=98–131 mm, TL=29–48 mm, HF=16.5–21 mm, EL=12–16 mm, CbL=25.3–30.8 mm, ZgW=12.5–17.5 mm, MxT=6.1–7.8 mm. M_1 with more massive anteroconid complex; LR5 usually absent.

Distribution. Mongolia.

SUBGENUS: *Yushanomys* new subgenus

Taxonomy. Contains a single species (*kikuchii*) which in the past was classified in *Volemys* (Zagorodnyuk 1990) or *Microtus* (s.lat.); in *Microtus*, *kikuchii* was considered a member of the *maximowiczii* group (Zimmermann 1964) or a close relative of *fortis* (Corbet & Hill 1992). Bannikova et al. (2010) allocated *kikuchii*, together with *oeconomus* and *montebelli*, to *Pallasiinus* (as a subgenus of *Alexandromys*); possibly, *kikuchii* holds basal position in *Alexandromys* (Steppan & Schenk 2017). The time of divergence of *kikuchii* is presumably 0.79 Mya (Bannikova et al. 2010).

Type species. *Microtus kikuchii* Kuroda, 1920.

Etimology. The name *Yushanomys* is composed of Yushan and the extension "mys" (μυς; from Ancient Greek) for "mouse", therefore a "mouse from Yushan". Yushan (also Yu-Shan) is the highest peak (3,952 m) in the Central Mountain Range of Taiwan, which is the habitat for *A. kikuchii.*

Diagnosis and Comparisons. *Yushanomys* differs from all other subgenera and species of *Alexandromys* by a combination of the following traits: (i) tail is very long (TL/H&B=0.55–0.80 vs <0.56 in remaining *Alexandromys*); (ii) females have 2 pairs of inguinal nipples (8 nipples in the genus); (iii) ears protrude above the fur like a wood-mouse; (iv) plantar and palmar pads are larger than in any other *Alexandromys* (Figures 203e, 204e); (v) whiskers are long (35 mm); (vi) the skull is narrow (ZgW/CbL=0.52–0.57; Figure 226); (vii) M^1–M^2 have asymmetric loops with over-extended lingual (M^1) or labial (M^2) segments (Figure 227b).

Alexandromys kikuchii (Kuroda, 1920) – Taiwan Grass Vole

Microtus Kikuchii Kuroda, 1920:36. Type locality: "about 10,000 ft. [3,048 m] above sea-level on Mt. Morrison [Mt. Yushan], Formosa [Taiwan]" (pp. 39 & 41).

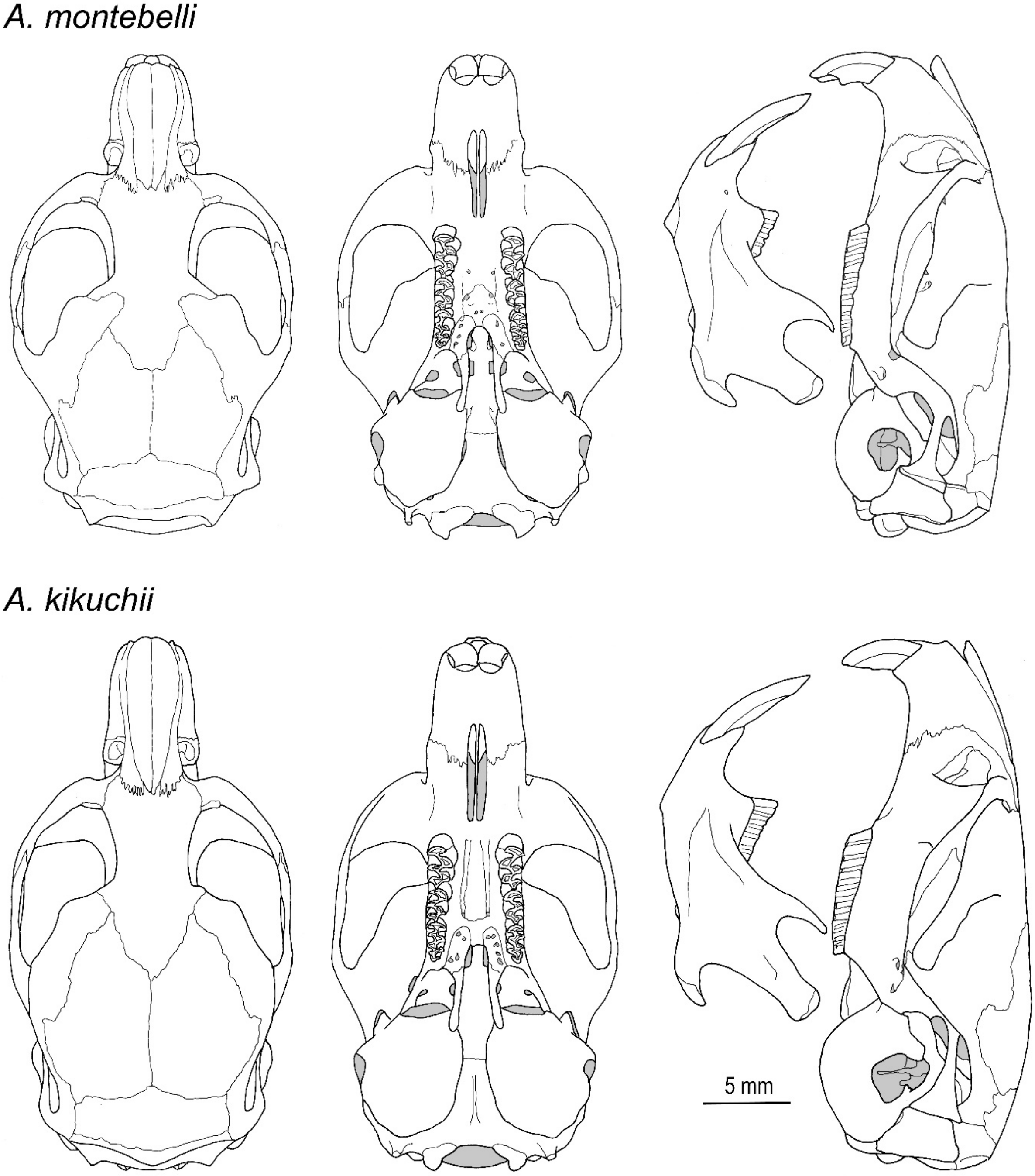


Figure 226: Skull and mandible of *Alexandromys montebelli* (top) and *A. kikuchii* (bottom).

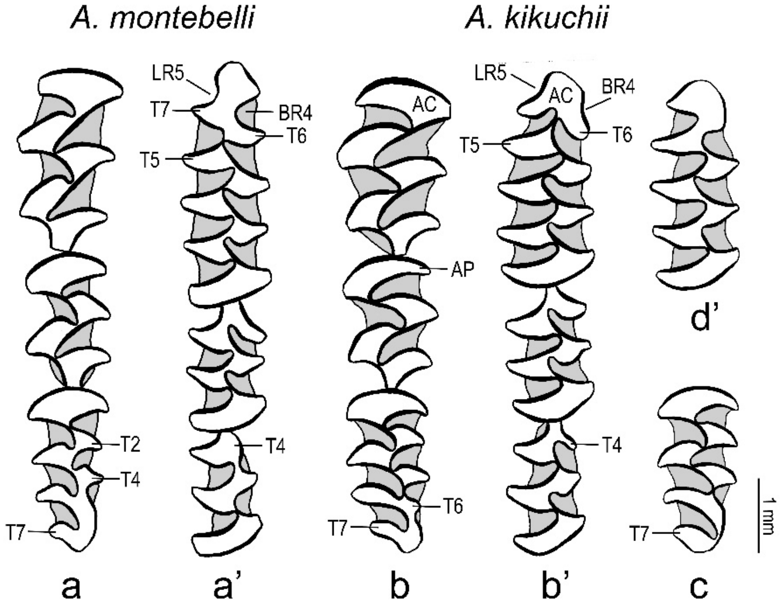


Figure 227: Molar pattern in *Alexandromys montebelli* (a,a') and *A. kikuchii* (b–d'). Pictured are upper (a,b) and lower (a',b') rows and isolated M^3 (c) and M_1 (d').

Distribution (Figure 228). Endemic to Taiwan and occupying one of the smallest ranges in the genus (area=3,460 km^2). The species is constrained to coniferous forests with undergrowth of bushy bamboos and shrubs high in the mountains (Yu 1994). Altitudinal range is 810–3,700 m but records are rare below 3,000 m.

Description. Dimensions: BWt=22–44 g, H&B=90–122 mm, TL=58–87 mm, HF=17.8–24 mm, EL=11.2–18 mm, CbL=26.3–31.2 mm, ZgW=13.8–16.8 mm, MxT=6.2–7.8 mm. Fur is soft and long (>10 mm and up to 17 mm; Aoki & Tanaka 1941); hairs do not conceal the annulation on the tail and the terminal pencil is short. There are 5 plantar and palmar pads. Fur is

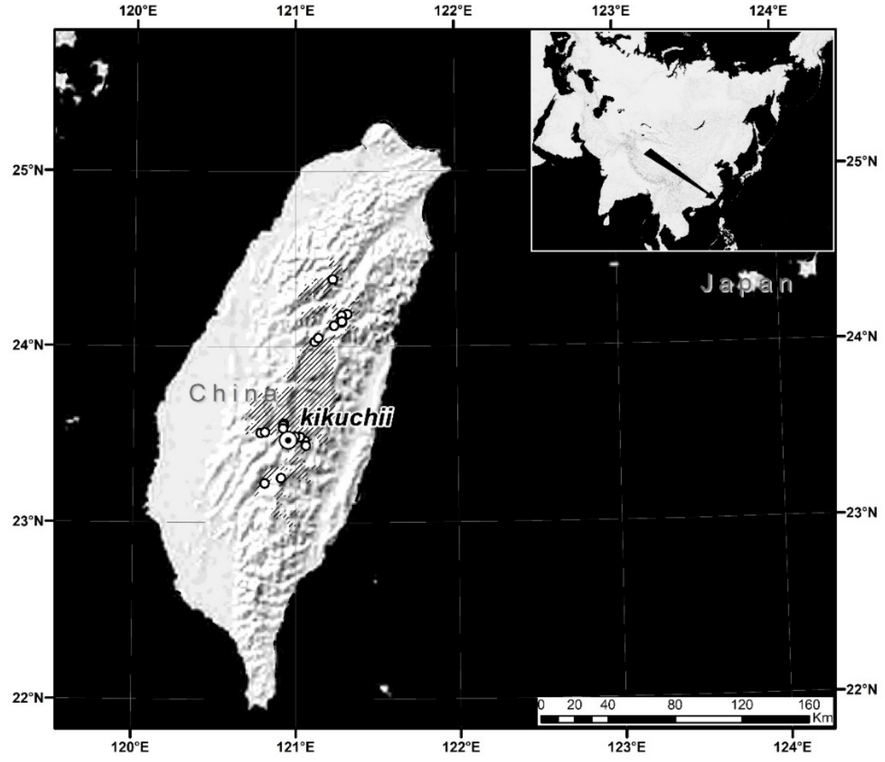


Figure 228: Distributional range of the Taiwan grass vole *Alexandromys kikuchii*.

ochraceous-buff, russet or wood-brown, not darkened towards the spine; flanks are light and shaded buffy and the underside is grey with a buffy shade. Paws are dirt-whitish to light grey, ears are brownish grey, and the tail is indistinctly bi-coloured, smoke grey above and lighter below. The skull is rather narrow and shallow with a large braincase. Interorbital region is wide and flat; supratemporal ridges are weak and rarely merge into a short and unremarkable sagittal crest in the posterior part of the interorbital constriction. Forehead is depressed behind the naso-frontal suture and between the diverging temporal ridges. Bullae are comparatively large (Figure 226). Molars are large and wide and the anterior lobes of M^1–M^2 are laterally stretched, hence their dentine spaces are usually reduced. M^3 has 3 (rarely 4) re-entrant angles on either side. M_1 has 3 outer and 4 inner re-entrant folds; additional anterior folds (LR5, BR4) are shallow. T5 is always isolated and T6 is widely confluent with the AC. T4 on M_3 is distinct although frequently narrow. Karyotype: 2n=30, NF_a=50; the X is medium-sized metacentric and the Y is one of the smallest acrocentrics (Harada et al. 1991, Mekada et al. 2001).

Variation and subspecies. Monotypic.

Alexandromys incertae sedis

Alexandromys montebelli (A. Milne Edwards, 1872) – Japanese Grass Vole

Arvicola montebelli A. Milne Edwards, 1872:285. Type locality: "Fusi-Yama", Honshu Island, Japan.

Synonyms. *[Eothenomys] Montebelloi:* Trouessart, 1897 [unjustified emendation of *montebelli* Milne Edwards]; *Arvicola hatanedzumi* Sasaki, 1904; *Microtus montebelli brevicorpus* Tokuda, 1933.

Taxonomy. Consistently treated as a species endemic to Japan (Aoki 1913, Kuroda 1938, and subsequent authors). Since the mid-1950s, Russian authors reported *montebelli* for Sakhalin and Shpanberg (known also as Shikotan; Kurille archipelago) (Sokolov 1952, Gromov & Baranova 1981) which was disproved by Reimers (1972). Bannikova et al. (2010) estimated the time of divergence for *montebelli* as 0.95 Mya and the earliest fossils in Japan are from the beginning of the late Middle Pleistocene (Kawamura 1989). Kawamura (l.c.) suggested immigration from Korea and some authors argued that *montebelli* is an insular vicariant of *maximowiczii* (Zimmermann 1964) or *oeconomus* (Yamakage et al. 1985). In the past *montebelli* was classified in the *arvalis* group or in *Pallasiinus* (as a subgenus of *Microtus*) together with *oeconomus* (Musser & Carleton 1993) and *limnophilus* (Zagorodnyuk 1990). Alexandromys *montebelli* and *kikuchii* are possibly basal in *Alexandromys* but their phylogenetic relationships have not yet been resolved.

Distribution (Figure 229). Endemic to the Japanese islands of Honshu, northern Kyushu, Sado and Notojima; the range covers an estimated 76,795 km². Present on Shikoku during the Late Pleistocene but vanished from there during the Holocene (Kawamura 1989) and is now absent (Kaneko 1982). A characteristic inhabitant of grassy and herbaceous cover in meadows, forest plantations and fields (Imaizumi 1960, Ota & Jameson 1961) from sea level up to 2,345 m a.s.l. Kaneko (1979) found *montebelli* in all habitats in western Honshu except in dense bamboo shrubs.

Description (Figure 202e). Dimensions: BWt=24–48 g, H&B=102–132 mm, TL=32–49 mm, HF=15–21 mm, EL=9.5–13.5 mm, CbL=25.6–28.8 mm, ZgW=14.4–16.8 mm, MxT=6.3–7.8 mm. A rather small grass vole with a moderately long tail (TL/H&B=0.30–0.45); males are heavier on average. Hair is soft, 7.5–10.5 mm long and lack sparse longer hairs, hence the colour is plain rather than grizzled; ears barely protrude from the fur. The tail is densely clad with whitish hairs which cover the annulation; the terminal pencil is short (2.5–5.5 mm) and always sparse. There are 5 palmar (Figure 203d) and 5 (rarely 6) plantar pads; pads are of approximately the same size (Figure 204d). The front claws are more slender than in the remaining grass voles. Dorsal pelage is brown (various tints of ochraceous tawny) with buffy or grey wash on the flanks; belly is grey. There is a great deal of individual variation in colouration. Tail is usually faintly bi-coloured, grey-brown to blackish brown above, grey below. Ears are grey; paws are lighter, usually whitish-grey. Baculum consists of proximal stalk (length×width=2.5×1.45

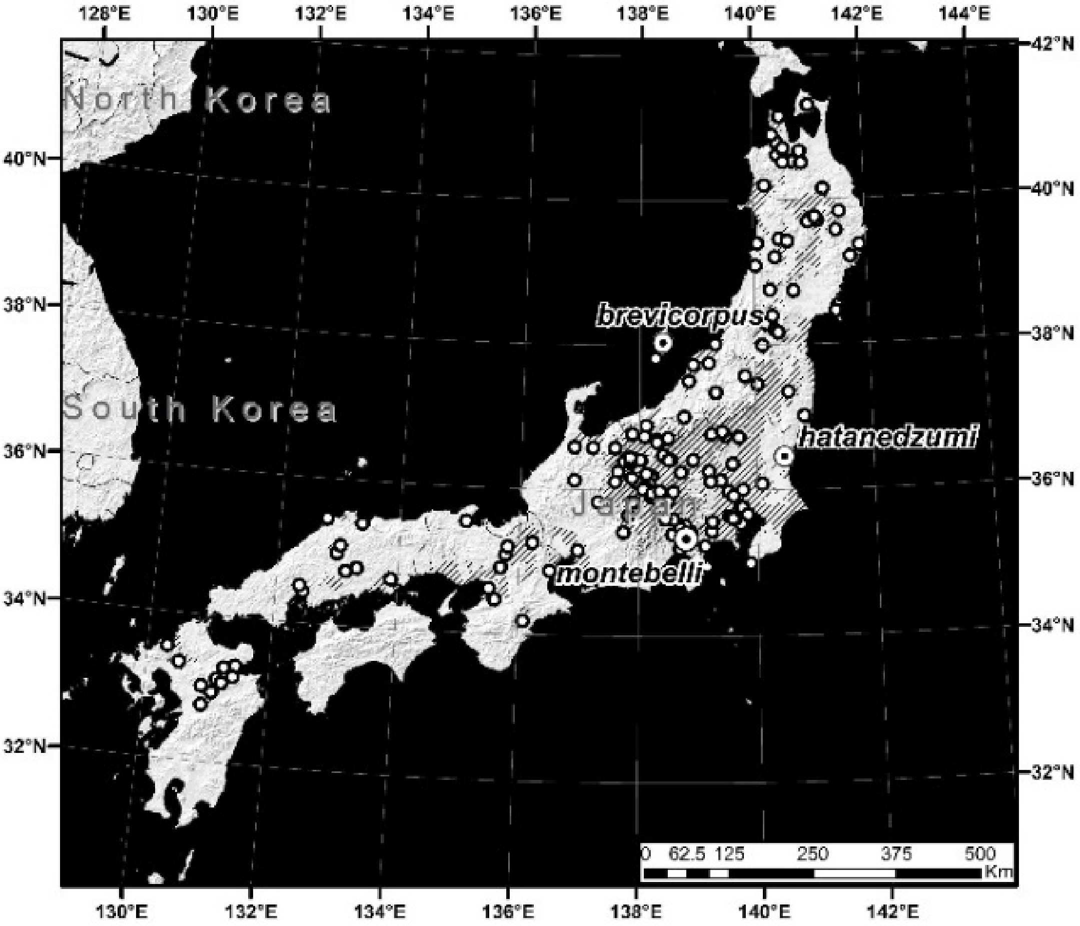


Figure 229: Distributional range of the Japanese grass vole *Alexandromys montebelli*.

mm) and distal trident (Yato & Motokawa 2021). The sperm head is falciform (Okada & Kageyama 2018). Skull is heavily built with a long braincase and short rostrum. Zygomatic arches run parallel and are not particularly bowed (ZgW/CbL=0.53–0.60). The nasals are bottle-shaped, expanded anteriorly but short and do not reach the plane of incisors. Squamosal bulges are moderate; supratemporal ridges are weak and the interorbital crest is invariably feeble. The dorsal profile of the skull is flat (Figure 226). M^3 has 3 labial re-entrant angles and 2 well-developed triangles (T2 and T4); an additional posterior triangle (T6) is invariably feeble when present. The lingual side has 3–4 re-entrant angles; in about half of cases T7 terminates the tooth posteriorly without being followed by a re-entrant angle and a posterior cap (Figure 227a). The anterior cap on M_1 is widely confluent with T6–T7; re-entrant angles BR4 and LR5 are shallow to moderately deep in the vast majority of cases; T5 is always isolated. T4 on M_3 is blunt and effectively absent. Morphotypes are detailed in Kawamura (1988, 1989). Karyotype: 2n=30, NF=56; all autosomes are bi-armed except one subtelocentric pair; X is medium-sized metacentric and Y is small acrocentric; the X and Y chromosomes are synaptic (Iwasa & Obara 1995). *A. montebelli* shares with *oeconomus* almost perfectly homologous G-bands in nearly all chromosomes (Yamakage et al. 1985).

Variation and subspecies. Size varies clinally and contradicts Bergmann's rule, hence the voles are smaller at high latitude and larger southwards (Kaneko 1988). The population from the Sado Is. was recognised in the past as a distinct subspecies (*brevicorpus*) on the basis of colouration, which is "more vivid ochraceous" (Tokuda 1941:60). Although the bright fur colouration of the type stands apart from dull voles from Honshu, the variation in both the Sado Island and the Honshu blurs the differences (Kaneko, personal communication). As a consequence, the Japanese grass vole is regarded as monotypic by the vast majority of authors.

GENUS: *Lasiopodomys* Lataste, 1887 – Hairy-footed Voles

Taxonomy. *Lasiopodomys* was proposed as a subgenus of *Microtus* and was treated this way for a considerable time. Miller (1896) combined *Lasiopodomys* with *Phaiomys* and Hinton (1926a) elevated it to the rank of genus. Hinton's view was hesitantly accepted in the 1940s (Ellerman 1941, Tokuda 1941) and started entering general use in the 1970s. Throughout the previous century the taxonomic content of *Lasiopodomys* remained fairly constant and similar to its current one.

Molecular phylogenetic reconstructions retrieved a sister position between *Lasiopodomys* and *Stenocranius* and some authors synonymise them. On the other hand, karyological evidence does not suggest a close association between these groups of voles (Agadzhanyan & Yatsenko 1984). Robovský et al. (2008:581) regarded a full-genus status for *Stenocranius* (without *Lasiopodomys*) as "the least problematic taxonomic solution" in their revision of arvicolines. The time of TMRCA for *Lasiopodomys–Stenocranius* is estimated at 1.53 Mya (Shi et al. 2021). We therefore continue to treat *Stenocranius* as a genus distinct from *Lasiopodomys*. The latter contains 2 monospecific subgenera with TMRCA dated to ~0.7 Mya (Li et al. 2017, Shi et al. 2021).

Distribution. Grasslands in eastern Asia: the Trans-Baykal regions (southern Chita and southern Buryatiya in Russia), Mongolia, Korea and north-eastern and central China as far south as the Yangtze Delta.

Characteristics. Robust voles with a deep head and small ears hidden in the fur. The tail is short (TL/H&B<0.30) and fully clad with stiff hairs which conceal the underlying annulation. Pelage is dense and of variable texture and length; colour varies from light sandy-grey to brown. Feet are broad and soles are densely hairy (Figure 230). Claws are long; longer on the front feet than the hind ones. Front claw III is ⅔ the length of the digit; the front thumb has a short pointed claw rather than a nail. Postero-lateral glands are situated on the hips (Quay 1968). Females have 8 nipples. Baculum is of a trident type; lateral distal digits are positioned posteriorly, reduced in size (length=0.15–0.25 mm), rarely ossify and are frequently absent (Aksenova 1980). Skull appears massive and broad; temporal ridges are developed (Figure 231). Bullae are of moderate size and internally filled with a dense spongy tissue. The mastoid portion is slightly inflated. Molar pattern is characterised by a simplified M_1 and M^3. The M_1 normally consists of 5 alternating triangles and a simple oval AC; rarely, an additional triangle T6 is present. M^3 has the AL, 2 alternating triangles and a simple posterior cap (Figure 232). Differentiation of the enamel is positive with the luff edge being much thicker than the lee edge. *Lasiopodomys* is characterised by a rate of chromosomal change which is extremely fast (~10 rearrangements per million years) even to arvicoline standards. Since their divergence, *brandtii* and *mandarinus* have undergone ~20 chromosomal changes (Gladkikh et al. 2016).

Key to species

1a) Fur is coarse and light (yellow); no demarcation on the flanks; tail is monochromatic; 6 (rarely 5) plantar pads; the braincase is <½ the skull length; interorbital constriction <3.9 mm; sagittal crest present in adults; nasals >8.0 mm; central distal baculum ~⅓ the length of proximal baculum ………..……….……....... *brandtii*
1b) Fur is soft and darker; light belly is sharply demarcated from brown back; tail is bi-coloured; 5 plantar pads; the braincase is ~½ the skull length; interorbital constriction >3.9 mm, without sagittal crest; nasals <8.0 mm; central distal baculum <¼ the length of proximal baculum ………………….…. *mandarinus*

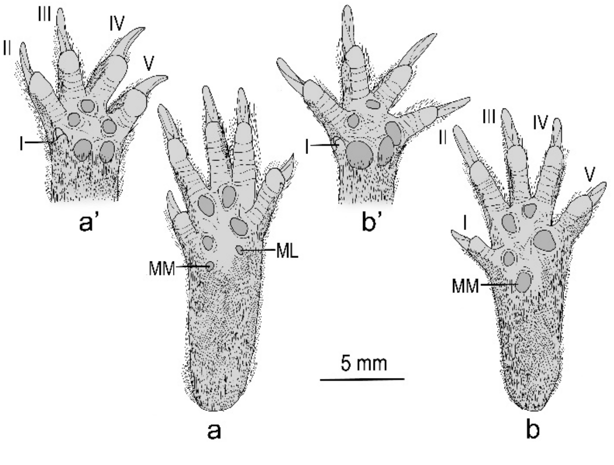
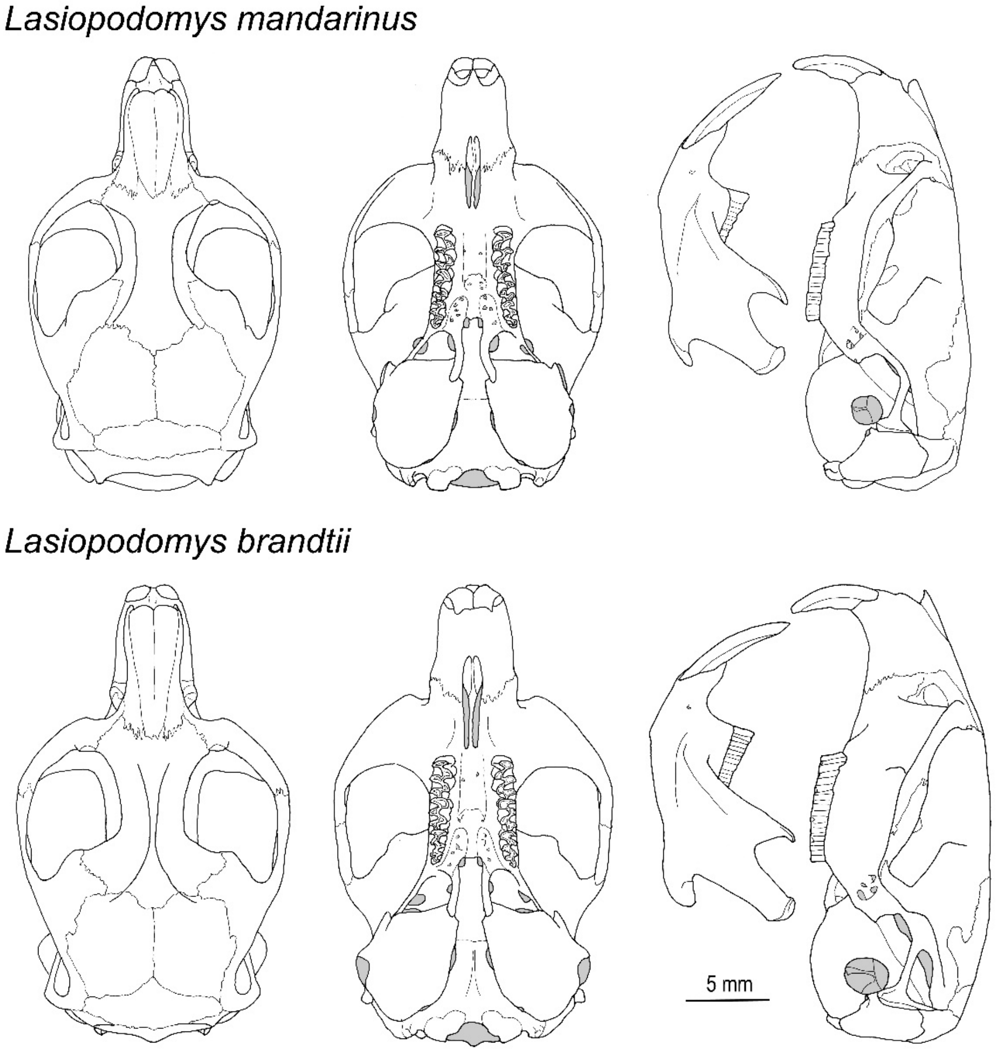


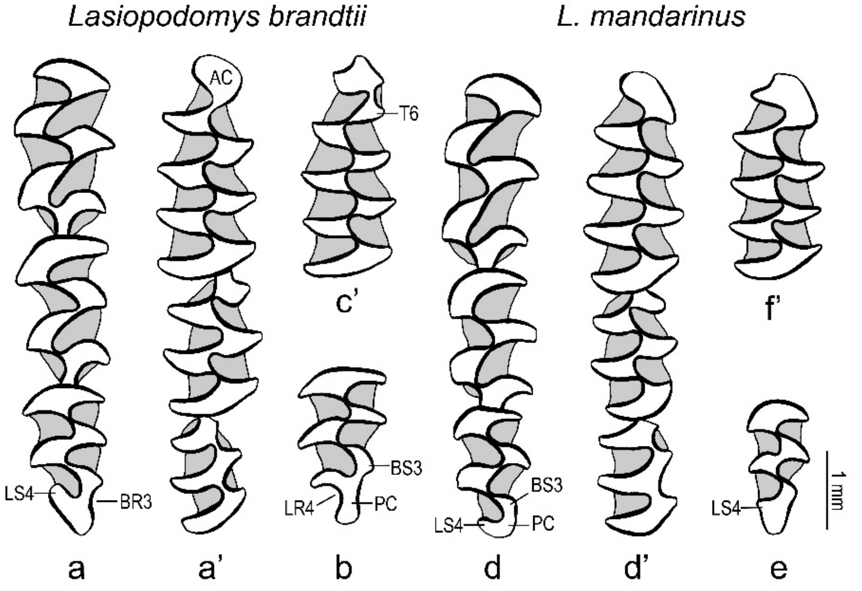
Figure 230: Left palm (a',b') and sole (a,b) in *Lasiopodomys brandtii* (a,a'–Mongolia) and *L. mandarinus* (b,b'– Chita, Russia).



Lasiopodomys mandarinus

Lasiopodomys brandtii

Figure 231: Skull in hairy-footed voles: *Lasiopodomys mandarinus* (top–central Mongolia) and *L. brandtii* (bottom–100km south-west of Ulaanbaatar, Mongolia).



Lasiopodomys brandtii

L. mandarinus

Figure 232: Molar pattern in hairy-footed voles. *Lasiopodomys brandtii*: upper (a) and lower row (a'–Mongolia, 100km south-west of Ulaanbaatar); isolated M^3 (b–Chita, Russia) and M_1 (c'–Mongolia, 100km south-west of Ulaanbaatar). *L. mandarinus*: upper (d) and lower row (d'– central Mongolia); isolated M^3 (e– Chita, Russian Federation) and M_1 (e'– Kolanchow, Shanxi, China).

SUBGENUS: *Lasiopodomys* Lataste, 1887

Lasiopodomys Lataste, 1887:269. Type species by monotypy is *Microtus brandti [=brandtii]* Radde.

Lasiopodomys brandtii (Radde, 1861) – Yellow (Brandt's) Hairy-footed Vole

Distribution (Figure 233). The area of distribution extends across 653,440 km^2 of south-eastern Chita (Russia), Mongolia (Arkhangay, Bayanhongor, Bulgan, Dornod, Dornogovi, Dundgovi, Dzavhan, Govi-Alaty, Govi-Sümber, Hentiy, Hovsgol, Omnogovi, Övörhangay, Selenga, Suhbaatar, Tov, Ulaanbaatar, and Uvs), central Nei Mongol and margins of Hebei and Jilin (China). The yellow vole occupies patchy, ephemeral grassland habitats with moderately high (5–17 cm) and dense vegetation (cover 40–80%; Zhang et al. 2003) hence the range is fragmented at the finer scale. Altitudinal range is 135–2,785 m. Strong multi-annual fluctuations in abundance are punctuated by local extinctions. Range expansion of up to 200 km was documented in Mongolia during the 2nd half of the 20th century (Dawaa et al. 2005). The Quaternary distribution was more extensive, encompassing the south-eastern shore of Lake Baikal in the north and crossing the 40th parallel in the south. The range started shrinking in the late Pleistocene and Holocene (Alexeeva et al. 2015). Fossils (Alexeeva et al. 2015) and phylogeographic evidence (Li et al. 2017) suggest the origin of *brandtii* in the south-eastern part of its current range in China.

Characteristics (Figure 234). Larger than *mandarinus* with large eyes; pinnae less reduced and densely clad with short hairs; the tail is short (TL/H&B=0.16–0.24) and has a moderate terminal pencil (length=5.4–7.5 mm). Palms are more slender than in *mandarinus* and the claws are grey. There are 6 plantar pads (Figure 230a); both metacarpal pads are tiny and the outer pad (ML) is absent in some individuals. Fur is short (4–6.5 mm), dense and rather coarse; longer sparse hairs measure 8–10.5 mm; winter fur is longer and softer. *L. brandtii* has lateral glands which are absent in *mandarinus*. Fur is sandy-yellow, washed grey and grizzled by light tips of long hairs; flanks are lighter and the transition towards the underside is blurred. The belly is light grey, washed whitish or cream and irregularly darkened by grey hair bases. The tail is uniformly pale buff with a whitish terminal pencil; the ears are creamy-buff and paws are

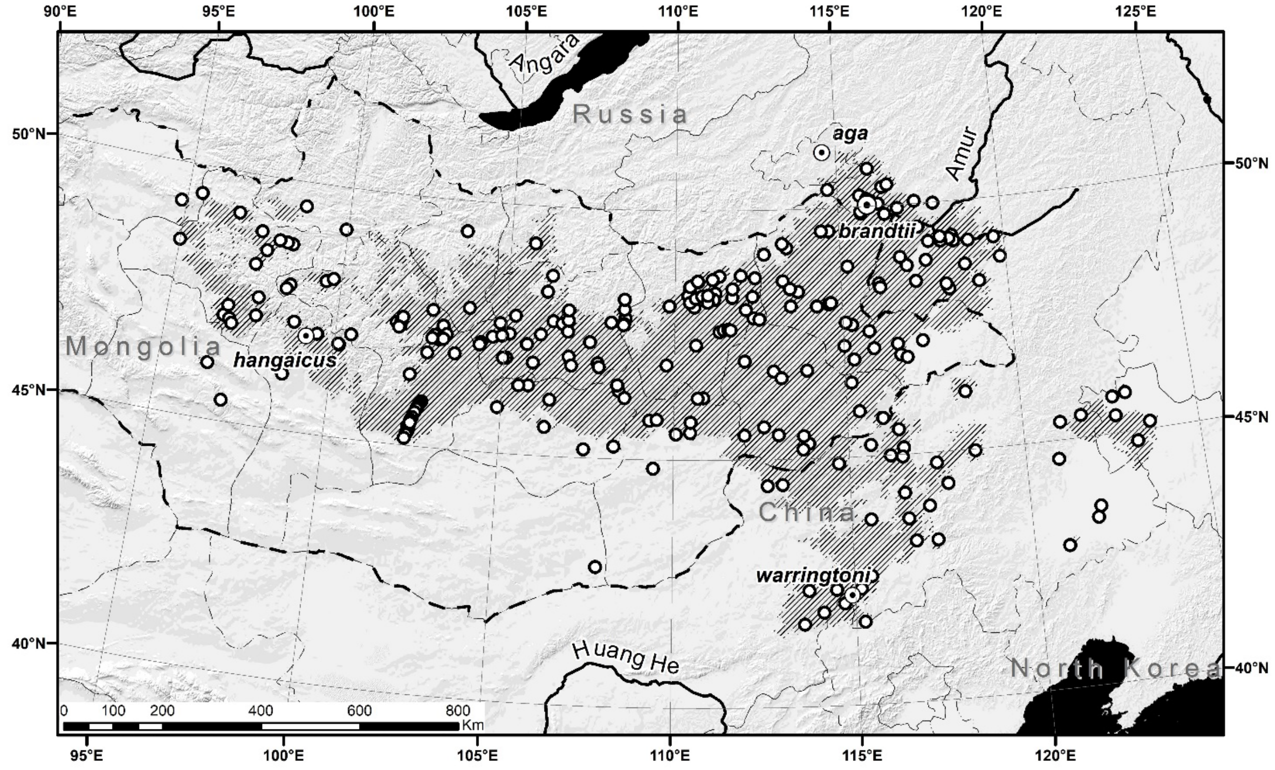


Figure 233: Distributional range of the yellow hairy-footed vole *Lasiopodomys brandtii*.

whitish. The proximal baculum is shorter than in *mandarinus* with a relatively broader base (length=2.4–3.0 mm, breadth =1.35–2.1 mm); the central distal baculum is longer (length=0.95–1.25 mm; Aksenova 1980).

Figure 234: Yellow (or Brandt's) hairy-footed vole *Lasiopodomys brandtii* from Mongolia. Photo: N. Nedyalkov.

The skull of *brandtii* is narrower relative to *mandarinus* (ZgW/CbL=0.55–0.63) and deeper (height behind M^3/CbL=0.36–0.38). The nasals are longer (length=8.0–9.0 mm) and the interorbital region is narrower (2.9–3.8 mm); the braincase is short and squarish. Incisive foramina are longer, posteriorly nearly approaching the level of M^1 alveoli; bullae are smaller (Figure 231). Temporal ridges merge into the interorbital crest which is most prominent in its posterior part. The mandibular body is deep, the coronoid and the angular processes are blunt; the alveolar process is feeble. The incisors are orthodont. Molar pattern is as in the genus. The PC of M^3 tends to be more complex than in *mandarinus*, occasionally having re-entrant angles LR4–BR3 and moderately developed salient angles LS4–BS3. M_1 is normally with 5 alternating triangles and a simple oval AC (Figure 232a–c'). In ~40% of individuals the anterio-buccal re-entrant angle BR4 forms and additional triangle T6; in <25% of such voles T6 is isolated from the AC (Alexeeva et al. 2015).

Karyotype: 2n=34, NF_a=62–64; one autosomal pair is classified either as acrocentric or bi-armed; all other autosomes are bi-armed. The Y is acrocentric and the X is the largest chromosome in the complement (Orlov et al. 1978).

Variation and subspecies. The molar pattern is remarkably homogeneous and conservative (Alexeeva et al. 2015). Two subspecies are recognised (Ognev 1950, Pardiñas et al. 2017) on the basis of colouration. Bannikov (1954) mapped their ranges in Mongolia.

Lasiopodomys brandtii brandtii (Radde, 1861)

Arvicola (Hypudaeus) brandtii Radde, 1861:683. Type locality: "vicinity of Tarei-nor [Tarei Lakes]", south-eastern Chita Oblast, Zabaykalskiy Krai, Russian Federation.

Synonyms. *Microtus brandti* var. *aga* Kashchenko, 1912; *Microtus warringtoni* Miller, 1913.

Distribution. The entire range except western Mongolia (see under *hangaicus*).

Characteristics. Dimensions: BWt=42–80 g, H&B=98–138 mm, TL=18–33 mm, HF=16.2–21 mm, EL=8.5–13.2 mm, CbL=25.0–29.1 mm, ZgW=14.3–17.2 mm, MxT=6.0–7.4 mm. The overall appearance is pale: light sandy-yellow back and belly with buffy tint.

Variation. The subspecies consists of 3 phylogeographic lineages: (i) Southeast lineage (south-central Nei Mongol), (ii) Northeast lineage (northern Nei Mongol and eastern Mongolia to the east of Hentiy), and (iii) West lineage (central Mongolia between Hentiy and Arkhangay. These lineages started diverging at an estimated 53 kya; genetic drift strongly overwhelmed the gene flow during their evolution (Li et al. 2017).

Lasiopodomys brandtii hangaicus (Bannikov, 1948)

Microtus (Lasiolodomys) brandti hangaicus Bannikov, 1948:24. Type locality: "Dzak-somon, south-western Khangai", western Mongolia.

Distribution. The westernmost segment of the range, to the west of the 102nd meridian. The range encompasses southern, south-western and western Khangay as far north as the Khan-Khukhey Ridge; the eastern border is on the Tuyn-Gol River (Bannikov 1953).

Characteristics. Dimensions: BWt=31–80 g, H&B=105–154 mm, TL=14–21 mm, HF=14–21 mm, EL=9–12 mm, CbL=26.5–29.9 mm, ZgW=15.3–17.8 mm, MxT=6.6–7.7 mm. Fur is duller without vivid shades. Back is greyish, flanks are buffy, and the belly is whitish to grey, without buffy wash. The ears are grey and contrast the surrounding fur; the paws are more grey than yellow; yellowish individuals are occasionally present which are indistinguishable from the nominal subspecies.

SUBGENUS: *Lemmimicrotus* Tokuda, 1941

Lemmimicrotus Tokuda, 1941:68. Type species is *Arvicola mandarinus* A. Milne Edwards.

Lasiopodomys mandarinus (A. Milne Edwards, 1871) – Mandarin Hairy-footed Vole

Taxonomy. Ellerman (1941) classified *mandarinus* into *Microtus* as the sole member of the *mandarinus* group adding that it "stands near *Lasiopodomys*." In the mid-20th century, Russian authors reported *mandarinus* under the name *vinogradovi*.

Distribution (Figure 235). The range covers an estimated 534,825 km^2 in Buryatia, Russia, and northern Mongolia (southern part of Gusinoye Lake Depression, Bargoy steppe, the Dzhida River the Selenga River; Smorkacheva 2001), and steppe habitats in river valleys of northern Khangay in central Mongolia (Arkhangay, Bulgan and Övörhangay; Dmitriev 1980). The remaining fragments are in the east and south-east: (iii) in western South Korea and (iv) in Jiangsu (China). Several small peripheral isolates are in north-eastern Nei Mongol, Liaoning, Beijing, Anhui, and eastern Hebei.

The mandarin vole is less xerophilous and more fossorial than Brandt's vole, seeking light soil in humid depressions with dense herbaceous cover (Xu 2016). Main habitats are fescue and feather-grass steppes in ravines, on sandy plains and finely grained rocky slopes (Borisova et al. 2001); also occupies grasslands in the forest zone and arable land. Altitudinal range is 5–1,650 m.

Characteristics. Smaller than *brandtii* with small eyes; pinnae are shortened, almost naked and hidden in the fur; the antitragus is low. The tail is short (TL/H&B=0.14–0.30) and well-haired; hairs conceal annulation. Palms are broader and the soles less hairy than in *brandtii*; there are 5 plantar pads and the only metatarsal (MM) pad is larger than in *brandtii;* Figure 230b). Claws are amber in colour and long: 4.0–4.5 mm on the fore feet and 3.0–3.9 mm in the hind feet. Fur is long (8–9.5 mm; sparse long hairs up to 10–13 mm), silky and dense. Colouration varies from light buff-brown to dark greyish-brown (see under subspecies); the underparts are grey and washed buffy-white to brownish-buff ; the throat is frequently white. Transition on the flanks is rather sharp. The tail is bi-coloured, brown above and light ochraceous to pure white below. Ears and paws are whitish to grey. The proximal baculum is longer than in *brandtii* with a relatively narrower base (length=2.85–3.55 mm, breadth =1.3–1.85 mm); the central distal baculum is shorter (length=0.45–0.7 mm) and the lateral distal digits are even more frequently absent than in *brandtii* (Tokuda 1941, Aksenova 1980).

Skull is wider than in *brandtii* (ZgW/CbL=0.59–0.67), nasals are shorter (6.2–8.0 mm), the interorbital region is wider (3.9–4.3 mm) and the braincase is longer (≈½ skull length) and shallower (height behind M^3/CbL=0.32–0.35). Incisive foramina are shorter and the bullae are larger (Figure 231). Temporal ridges remain far apart and separated by a groove. The braincase is ridged behind the squamosal notch. The mandibular body is low, the coronoid process is longer and the angular process is slim and sickle-shaped; the alveolar process is more prominent. The incisors are proodont. Molar pattern as in *brandtii* except that the heel on M^3 is even more simplified without a trace of re-entrant angles LR4–BR3, and with frail salient angles LS4–BS3 (Figure 232d,e).

The karyotype is polymorphic (2n=47–55) and at least 2 autosomal pairs show variation in morphology. The sex chromosome system is unusual with XX and X0 females and XY males. Furthermore, there are three types of novel X-chromosomes resulting from at least 2 independent translocations from the autosomes (Gladkikh et al. 2016, Romanenko et al. 2020). Sex determination is independent of the *Sry* gene on the Y chromosome (Chen et al. 2008); heterosomes are synaptonemal (Gu et al. 1999).

Variation and subspecies. Five subspecies are usually recognised (Allen 1940, Luo et al. 2000, Pardiñas et al. 2017). There have been attempts to link spatial chromosomal variation with subspecific taxonomy (e.g. Gladkikh et al. 2016, Romanenko et al. 2020).

Lasiopodomys mandarinus mandarinus (A. Milne-Edwards, 1871)

Arvicola mandarinus A. Milne Edwards, 1871:129. Type locality: "Chinese Mongolia"; restricted to "Shansi [Shanxi], probably near Saratsi" (Allen 1924:8), China.

Synonyms. *Microtus pullus* Miller, 1911.

Distribution. Central China (southern Nei Mongol, Shanxi, Shaanxi, Henan, and north-eastern Anhui).

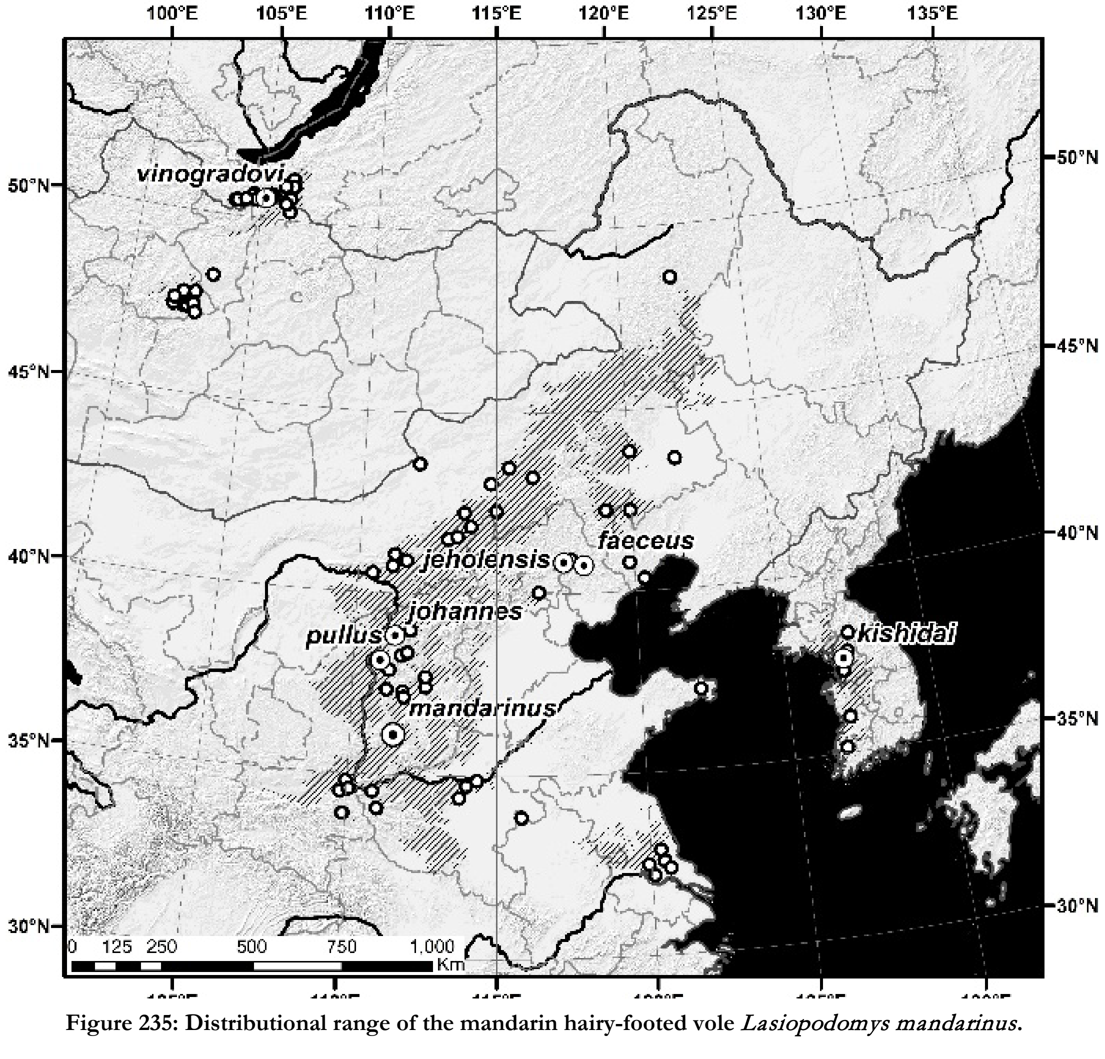


Figure 235: Distributional range of the mandarin hairy-footed vole *Lasiopodomys mandarinus*.

Characteristics. Dimensions: H&B=97–113 mm, TL=20–27 mm, HF=16–18 mm, EL=7–12 mm, CbL=24.7–27.4 mm, ZgW=15.0–17.7 mm, MxT=5.8–6.5 mm. Pelage is lighter, ventral hairs are tipped whitish. Back is pale hazel-brown, finely grizzled by black hairs along the spine which are sparse on the flanks. Ventral side is light cream-buff clouded by slate hair bases. Feet are dull buffy-white, tail is brownish above, whitish below. Aksenova (1980) found no difference in the morphology of the baculum between mandarin voles from Buryatiya (ssp. *vinogradovi*) and Arkhangay in central Mongolia (ssp. *mandarinus*). Karyotype: 2n=48–52; 2 pairs of autosomes are metacentric (Romanenko et al. 2020).

Lasiopodomys mandarinus johannes (Thomas, 1910)

Microtis johannes Thomas, 1910a:26. Type locality: "Mts. [Mountains] 12 miles [19 km] N.W. of Ko-lan-chow [Kelan], Shan-si [Shanxi], Alt[itude] 7,000' [2,135 m]" (Thomas 1910b:637), China.

Distribution. Restricted to the vicinity of Kelan and Ningwu (north-eastern Shanxi).

Characteristics. Similar to ssp. *mandarinus* but ligher and smaller on average. Dimensions: H&B=88–104 mm, TL=21–24 mm, HF=15.5–17 mm, EL=7–9 mm, CbL=23.7–27.4 mm, ZgW=14.5–17.8 mm, MxT=5.7–6.6 mm. Back is pallid ochraceous-buff and lacks all-black hairs; flanks are buff. Belly is pale buffy-white clouded by grey-slate hair bases. Tail is buffy above, dull white below; feet are dull whitish.

Lasiopodomys mandarinus faeceus (G. Allen, I924)

Microtus mandarinus fæceus G. M. Allen, 1924:8. Type locality: "Chili Province, 100 miles [160 km] northeast of Peking [Beijing], China."

Synonyms. *Microtus jeholensis* Mori, 1939.

Distribution. Eastern China: south-eastern Nei Mongol, Hebei, western Liaoning, Beijing, Shandong and Jiangsu.

Characteristics. Dimensions: BWt=23–35 g, H&B=86–112 mm, TL=15–24 mm, HF=14.6–17 mm, EL=8–11 mm, CbL=24.2–26.7 mm, ZgW=14.8–17.1 mm, MxT=5.6–6.3 mm. Similar to ssp. *mandarinus* but darker and with the ventral side washed buffy. Dorsal fur is brown and interspersed with all-black hairs; flanks are warm-buff. Underside is slaty-grey with a strong buff wash on chests and belly. Ventral hairs lack the whitish hair tips which are characteristic of ssp. *mandarinus*. Tail is brown above, buffy below; feet are dusky. Karyotype: 2n=47–50; 2 pairs of autosomes are metacentric (Romanenko et al. 2020).

Lasiopodomys mandarinus kishidai (Mori, 1930)

Microtus kishidai Mori, 1930b:53. Type locality: "Seiryo-Ri, near Keijo, Korea", now Seoul, South Korea.

Taxonomy. Described as a species and treated this way in Won (1968); synonymised with *mandarinus* by Ellerman & Morrison-Scott (1951).

Distribution. Endemic to the Korean Peninsula where it was only confirmed in South Korea, specifically in the northern part of the country; possibly present in adjacent areas of southern North Korea. There are a further 2 small isolates in south-western South Korea. Jones & Johnson (1965:378) reported an individual "trapped adjacent to the marshy area in a place overgrown with rank grasses." Rare subspecies.

Characteristics. Dimensions: H&B=88–120 mm, TL=20–28 mm, HF=15–18 mm, EL=5–11 mm, CbL=26.5–26.9 mm, ZgW=16.3–18.0 mm, MxT=6.6–7.0 mm. The darkest subspecies: dorsal pelage is neutral grey, underside is slate; inner surface of pinnae and paws whitish, the tail is brown.

Lasiopodomys mandarinus vinogradovi (Fetisov, 1936)

Microtus (Lasiopodomys) vinogradovi Fetisov, 1936:125. Type locality subsequently restricted to "Burgultay R[iver] in Dzhidinski rayon, Western Transbaikal" (Ognev 1950:345).

Distribution. The isolate in Buryatia and adjacent north-central Mongolia.

Characteristics. Dimensions: BWt=19–45 g, H&B=89–132 mm, TL=14–28 mm, HF=14–19 mm, EL=6–11 mm, CbL=23.3–27.8 mm, ZgW=13.2–16.8 mm, MxT=5.8–7.2 mm. Dark subspecies. Dorsal fur is greyish-brown, occasionally washed rusty and finely grizzled with buffy hair tips. Grizzling effect becomes less obvious along the flanks which are light-brown to buffy; the transition is sharp. Belly is grey and washed cream, buffy or whitish. Tail is dark grey to blackish-brown above, whitish or light grey below; ears and feet are grey. Karyotype: 2n=47–48; 3 pairs of autosomes are metacentric (Romanenko et al. 2020).

GENUS: *Stenocranius* Kashchenko, 1901 – Narrow-headed Voles

Stenocranius Kashchenko, 1901:167. Type species is "*Microtus (Stenocranius) slowzowi* Poljak[ov]" [= *Mus gregalis* Pallas].

Taxonomy. *Stenocranius* was established as a subgenus of *Microtus* and since the late 1940s has been ranked as a genus in its own right (Dunaeva 1948, Kuznetsov 1948b). We continue this practice although *Stenocranius* is frequently regarded as a subgenus of *Lasiopodimys* (see under the latter).

For most of the 20th century, voles with pronouncedly narrowed skulls and short hairy tails on both sides of the Bering Strait were treated as being closely related. The idea dates back to Miller (1899c) but Nelson (1931) first classified the Nearctic *Microtus muriei* Nelson, 1931 (a synonym of *M. miurus* Osgood, 1901) into the subgenus *Stenocranius*. Subsequently, Rausch (1964) synonymised *miurus* with *gregalis,* which was refuted shortly afterwards on the grounds of karyological evidence (Liapounova & Mirokhanov 1969). The name *Stenocranius* remained in use for Nearctic narrow-headed voles into the 1980s (e.g. Honacki et al. 1982) until Conroy & Cook (2000) demonstrated the Nearctic origin of *miurus* and refuted its putatively close relationships with *gregalis*.

In the early 20th century *Stenocranius* was regarded as polytypic with a number of recognised species varying between 2 species (Vinogradov 1933, Allen 1940) and 7 species (Ognev 1923). Since the early 1940s a single Palaearctic species was recognised in *Stenocranius* (Vinogradov & Argyropulo 1941, Kuznetzov 1944) and this view persisted for more than half a century. A recent phylogeographic analysis based on *Cytb*-gene and nuclear markers (Petrova et al. 2015, 2016) retrieved a cryptic species (*raddei*) from the upper reaches of the Amur River at the south-eastern edge of the species range. TMRCA for *gregalis* and *raddei* was estimated at 0.7–0.8 Mya. Crossbreeding trials between 2 mitochondrial lineages of *gregalis* (A, B; see below under *gregalis*) and *raddei* yielded offspring only in crosses *gregalis* B×*raddei*; viability of hybrids was reduced and only some of the females were fertile (Petrova et al. 2016).

Distribution. The range is more fragmented and patchy than in any other arvicoline. Narrow-headed voles are present in north-eastern European Russia, Siberia, Kazakhstan, Kyrgyzstan, northern Mongolia, and north-western, northern and eastern China (Shenbrot & Krasnov 2005).

Characteristics (Figure 236). Externally narrow-headed voles closely resemble *Microtus arvalis*. The eyes are characteristically small and the ears overtop the fur. The tail is short (TL/H&B<0.30), densely haired and usually with a long terminal pencil; the annulation is hidden by hairs. There are 6 (rarely 5) plantar pads; the pollex has a nail and the remaining digits have prominent claws (Figure 237). Posterolateral glands are situated on the flanks. Texture and length of fur as well as colouration vary between populations. Back can be of nearly any hue between light-drab or light yellowish-grey to dark brown-grey; basic colour is always grizzled by an admixture of light (buffy to whitish) and black hair tips. Winter pelage tends to be lighter and young voles are greyer. There can be a broad and faint medial stripe of

Figure 236: Common narrow-headed vole *Stenocranius gregalis* from the Urals. Photo courtesy Dina Nesterkova.

variable length stretching anywhere between the frontal region and the midback. Flanks are usually lighter and more buff; the colour of the back and underside gradually shade into each other in dark animals but the demarcation can be distinct in light-coloured individuals. The belly varies from light whitish grey to grey or slate; usually it is washed buffy or rusty. Females have 4 pairs of nipples. Baculum is of trident type with vestigial or absent lateral distal digits.

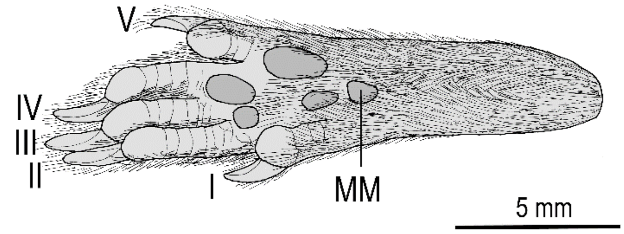


Figure 237: Left palm in *Stenocranius gregalis* (near Aktash, Altay Republic, Russia).

The skull is unique among Palaearctic arvicolines due to its narrow and slender shape (Figure 238). Instead of spreading evenly zygomatic arches bow anteriorly at the zygomatic root and afterwards run nearly parallel; the breadth across zygomatic arches (ZgW/CbL=0.43–0.56) is wider than the braincase by 5–25%. The orbital region is long and narrow; the interorbital constriction is <3.2 mm in all populations except the largest Arctic voles. The sagittal ridge is prominent and long. The braincase is long (~½ the skull length) and the nasals are short (<¼ the skull length). Incisive foramina are short to moderately long; palatal grooves are prominent, the postero-lateral pits are deep and the medial septum is markedly narrow. Bullae are of average size. The skull is moderately deep and the dorsal profile is concave between the nasals and the parietals. The mandible shows no peculiarities; the coronoid process is long and the alveolar process is present as a shallow swelling. Incisors are orthodont and the molars have an elongated appearance. M^3 normally has 3–4 inner and 3 outer salient angles. M_1 has 5–7 closed triangles between the posterior prism and the anterior cap (Figure 239).

Key to species

Because of the high morphological variability of *gregalis* throughout its extensive range, the key is valid for the Transbaikal region.

1a) Dorsal pelage is dark, grey-brown; M^3 usually with 4 lingual salient angles ………………………..…. *gregalis*
1b) Dorsal pelage is buff or light buff; M^3 usually with 3 lingual salient angles …………………………..…… *raddei*

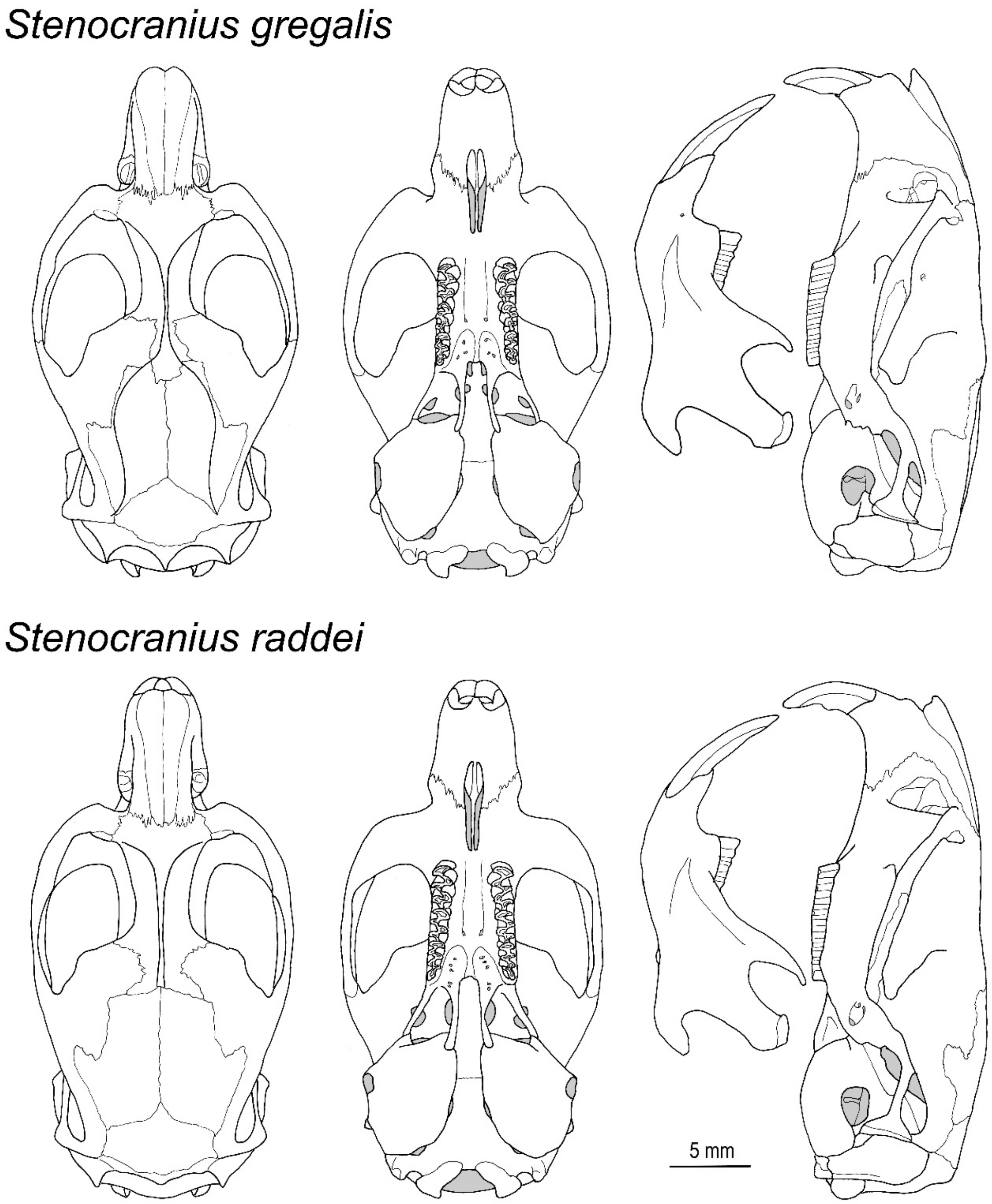


Figure 238: Skull in narrow-headed voles: *Stenocranius gregalis* (Kuray Steppe, Altay Republic, Russia) and *S. raddei* (Kuytyn, Krasnokamenskiy rayon, Zabaykalsky Krai, Russia).

Stenocranius gregalis (Pallas, 1779) – Common Narrow-headed Vole

Mus gregalis Pallas, 1779:238. Type locality: "orientali Sibiria", "Tschulymum" etc.; restricted to the vicinity of "Chulym", a right tributary of the Ob' River where Pallas first saw narrow-headed voles (Ognev 1950:475). The type locality is in the Novosibirsk Oblast, Russia (Pavlinov & Rossolimo 1987:202).

Synonyms. *Arvicola Eversmannii* Polyakov, 1881; *Arvicola Nordenskiöldii* Polyakov, 1881; *Arv[icola] arvalis* var. *Slowzowii* Polyakov, 1881; *Microtus tianschanicus* Büchner, 1889; *Microtus ravidulus* Miller, 1899; *[Microtus (Stenocranius) slowzowi*] var. *lutea* Kashchenko, 1901;

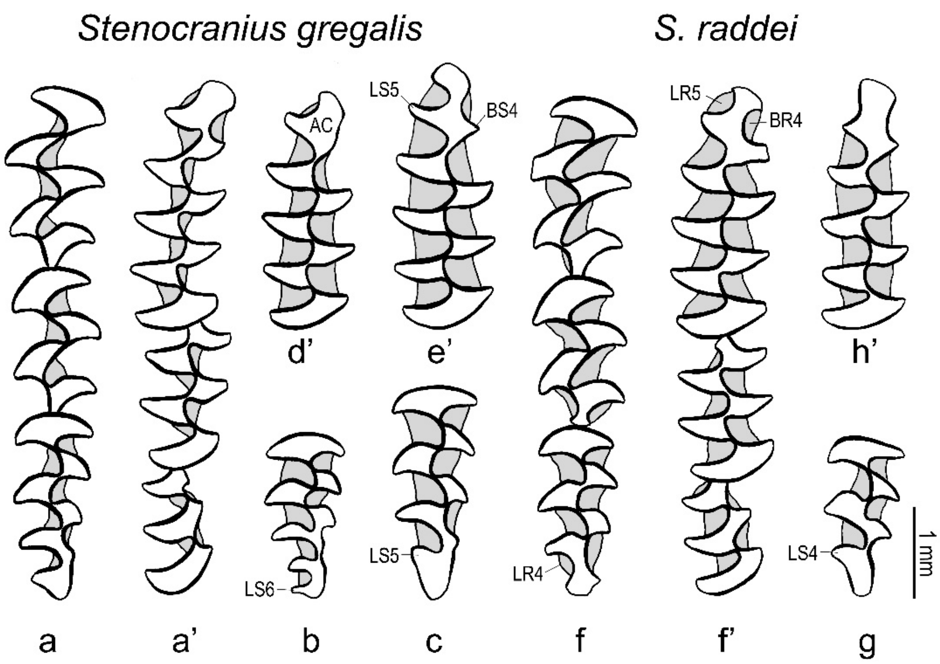


Figure 239: Molar pattern in narrow-headed voles (all from Russian Federation). *Stenocranius gregalis*: upper (a) and lower row (a'–Sretensk, Zabaykalsky Krai); isolated M^3 (b–Alan River, Sakha; c–Dalay Nor, Zabaykalsky Krai) and M_1 (d'–Sretensk; e'–Yana River, Sakha). *S. raddei*: upper (d) and lower row (d'–Kuytyn, Krasnokamenskiy Rayon, Zabaykalsky Krai,); isolated M^3 (e–Tsagan Nor, Aginsky-Bryatskiy District, Zabaykalsky Krai) and M_1 (f'–Matsiyevskaya Station, Borzinskiy District, Zabaykalsky Krai).

[Microtus (Stenocranius) slowzowi] var. *tridenticulata* Kashchenko, 1901 [nomen nudum]; *[Microtus (Stenocranius) slowzowi]* var. *brevicauda* Kashchenko, 1901; *M[icrotus] gregalis pallasii* Kashchenko, 1901 [nomen oblitum]; *Microtus angustus* Thomas, 1908; *Stenocranius buturlini* Ognev, 1922; *Microtus (Stenocranius) castaneus* Kashkarov, 1923; *Stenocranius kossogolicus* Ognev, 1923; *Stenocranius major* Ognev, 1923; *Microtus (Stenocranius) gregalis montosus* Argyropulo, 1932; *S[tenocranius] g[regalis] unguiculatus* Vinogradov, 1935; *Microtus (Stenocranius) gregalis dolguschini* Afanasiev, 1939; *Microtus (Stenocranius) gregalis tarbagataicus* Ognev, 1944; *Microtus (Stenocranius) gregalis tundrae* Ognev, 1944; *Microtus gregalis talassicus* Heptner, 1948 [substitute name for *castaneus* Kashkarov]; *Microtus (Stenocranius) gregalis zachvatkini* Heptner, 1945; *Microtus (Stenocranius) gregalis dukelskiae* Ognev, 1950; *Microtus gregalis sirtalaensis* Ma, 1966 [not Young; Corbet 1978:116, Musser & Carleton 2005:998].

Distribution (Figure 240). The common narrow-headed vole occupies the vast majority of the range of *Stenocranius* with the area covering 5,274,338 km². The taiga forest zone fragments the distribution into 3 segments in (i) the northern (tundra), (ii) the central (cold steppes of central Sakha) and (iii) the southern (forest-steppes, plain and mountain steppes, and semideserts). The tundra populations to the north of the taiga are in 5 fragments (west-to-east): (i) south-west of Arkhangelsk (Tundra Station) which is the westernmost occupancy of the species, (ii) between the River Pechora and Yamal, (iii) from Taymyr eastward to the Olenek River, (iv) in the lower reaches of the Lena River, and (v) between the Yana and Kolyma Rivers. The common narrow-headed vole was also recorded on the southern Novaya Zemlya, Vaygach Is. (between the Novaya Zemlya and the mainland), and Bely Is. (offshore of the Yamal Peninsula). Another major segment is located in cold steppes on permafrost in eastern Siberia along the central course of the Lena River and its major tributaries, the Aldan and Vilyuy. The last major fragment occupies a wide zone of forest-steppes, steppes and semi-deserts to the south of the taiga between the south-eastern slopes of the Ural Mts. and the mid-reaches of the Amur River in south-western Siberia (Russia), northern Kazakhstan, Altai (in the Altai Republic and Altai Krai of Russia, and in north-western Mongolia), and the Sayan Mts. (Russian part of southern Siberia), northern, central, and eastern Mongolia, and near north-western China (Nei Mongol, Hebei, Heilongjiang). Peripheral isolates are scattered around

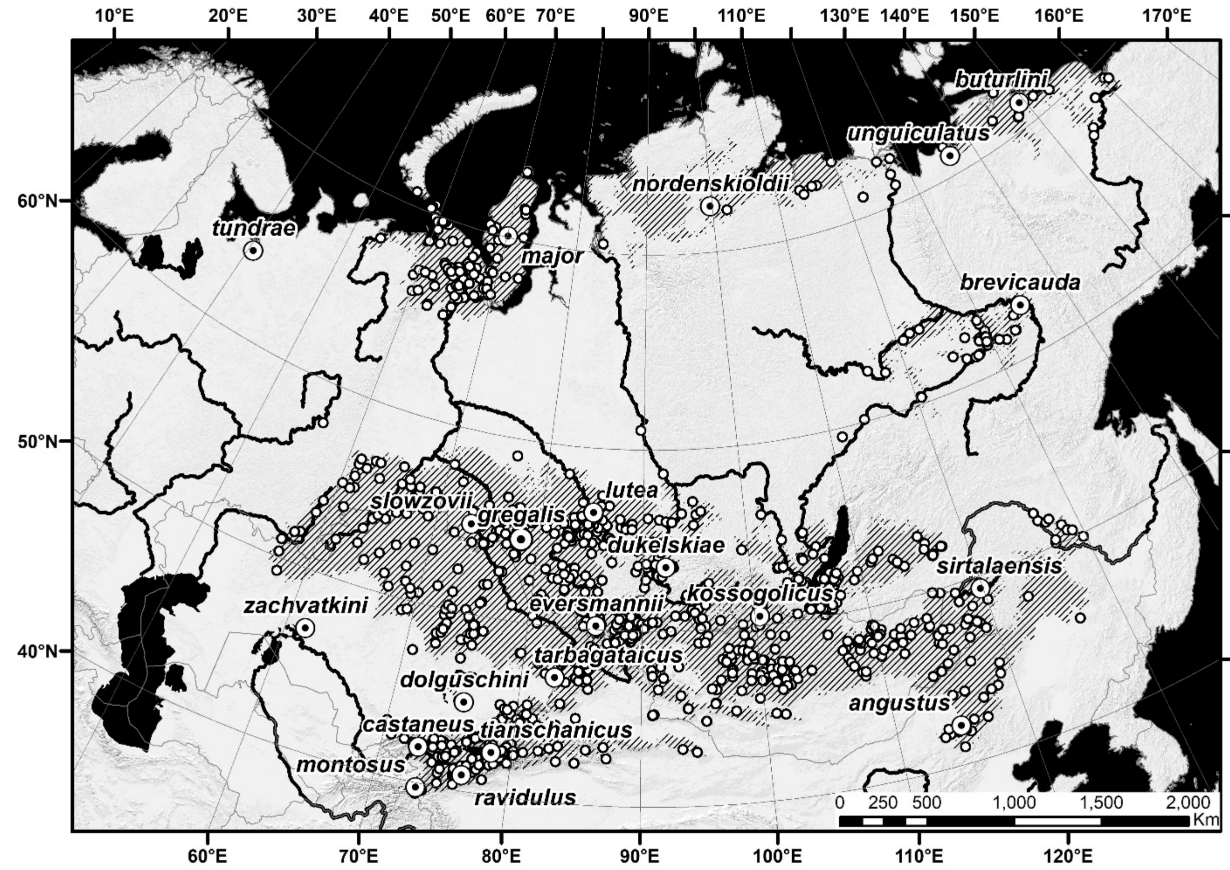


Figure 240: Distributional range of the Common narrow-headed vole *Stenocranius gregalis*.

this belt. The largest isolates are (i) north of the Cis-Baikal region (Russia) in the upper parts of Angara and Lena River basins, and (ii) south of the Tien Shan Mts. between (west-to-east) Karatau (Kazakhstan) and Barkol (China, Xinjiang). The latter fragment includes the Tien Shan, Trans-Ili Alatau, Terskey Alatau, Dzungarskiy Alatau, Alay and Trans-Alay Ridges in Kyrgyzstan, eastern Kazakhstan and Xinjang (China); this fragment nearly reaches northern Pamir, however the vole is absent from Pamir proper. Numerous smaller isolates are in (i) the forest-steppes of the Kama River basin (western slope of the Ural Mts., Perm, Russia) and further north; (ii) Vasyugan River basin (Tomsk Oblast, Russia), (iii) the central Yenisey River valley (Krasnoyarskiy Krai, Russia), (iv) vicinity of the Aral Sea (Kyzyl-Orda, Kazakhstan), (v) the proximity of Lake Balkhash (lower part of the Ili River valley, Almaty, south-eastern Kazakhstan), (vi) Baitag-Bogdo Mts. (Hovd, bordering south-western Mongolia–Xinjiang, China) and (vii) Aj-Bogdo Mts. (Govi-Altai, southern Mongolia). An isolate along the lower Yellow River in Henan (China), mapped in Zhang et al. (1997), is not reported by subsequent Chinese authors (Luo et al. 2000, Wang 2003, Jiang et al. 2015), and is not shown in Figure 240.

The common narrow-headed vole lives in meadows and shrubby stands in an open landscape (e.g. Kislyi et al. 2022). It avoids marshy situations in the Polar zone but further south where it is exposed to increased aridity it seeks proximity to water in river valleys and on lake shores. In the taiga zone, voles occupy dense pine forests, forest clearings and arable land; further north they enter houses and barns. In the tundra the range is fragmented to a small scale with a distance of 2–6 km between population patches (Dobrinsky & Sosin 1981). Altitudinal range is from sea level to 4,355 m.

Characteristics. Dimensions: BWt=29–70 g, H&B=98–139 mm, TL=17–39 mm, HF=14–19 mm, EL=8–16 mm, CbL=23.5–29.8 mm, ZgW=10.4–16.6 mm, MxT=5.2–7.7 mm. Interpopulation variation in colour and fur texture is covered below. The proximal baculum is 1.95–3.15 mm long and 1.10–1.85 mm wide; the basal outline is trilobate. The median distal baculum is relatively long, accounting for >⅓ the proximal baculum. Lateral digits usually remain cartilaginous (in 84% of cases studied by Aksenova 1983) or are entirely absent (16%); their ossification is delayed to the age of 3–5 months; when osseous, the lateral digits are short (length=0.20–0.40 mm; Aksenova 1983).

The antero-basilar part of the occipital bone and the bullae are narrower than in *raddei*. The common morphotypes of M_1 (Figure 239a,d') account for ~80% of cases and the frequency of the trifoliate type is always <50% (Dupal & Abramov 2010). In Central Siberia, Ekimov & Uglova (2012) distinguished 15 M_1 morphotypes and each was found in every local population provided the sample was large enough. In comparison with *raddei, gregalis* tends towards less deep re-entrant angles LR5 and BR4; the overlap, however, is considerable. The M^3 is more complex than in *raddei*, usually with 4 inner salient angles and a longer posterior cap; 3 inner angles can be frequent in some populations.

Karyotype: 2n=36, NF_a=50; 8 pairs of autosomes are bi-armed and 9 pairs are telocentric; X is large metacentric and Y is telocentric. The karyotype was formed by 10 fusions and 1 fission of ancestral chromosomal elements (Lemskaya et al. 2010). Some populations from Mongolia have 1–4 acrocentric supernumerary (B) chromosomes (2n=36–40; Koval'skaya 1989) but no other variation was found.

Variation and subspecies. The common narrow-headed vole exerts a strong individual and geographic variation in size, proportions, colour and texture of fur. Voles living in the European Arctic, Polar Urals, Yamal, and the Ob' Delta (*tundrae* and *major*) have long (10.5–16.5 mm), fluffy and soft fur, a densely furry tail with a long terminal pencil (up to 14–16 mm; Figure 241a), and hairy soles and palms. Front claws tend to be longer. Dorsal fur is yellowish-grey, cinnamon-buff or buffy-brown and a stripe is rarely present. The flanks are lighter and the underside is whitish-grey, clouded with slate underhair. The tail is short and bi-coloured, above light grey with a heavy yellowish or rusty wash, below dirty white to pure white; paws are silver or whitish. Narrow-headed voles from the tundra between Taymyr and Kolyma Delta (*nordenskioldii*, *buturlini* and *unguiculatus*) are darker with grizzled-tawny to grey-brown dorsal pelage. To the south of the taiga zone the pelage is darker in the forest-steppe zone and lighter in more arid environments. Dorsal side is anywhere between buffy-brown, brown-grey and bistre, grizzled by light (whitish or buffy) and black hair-tips; the presence of a stripe varies among populations. The belly is dirty white with slate hair bases showing through and frequently washed buffy or rusty. Texture of the fur is soft to slightly coarse; hair is 5.5–15 mm long (usually 9–12 mm). The tail is less densely clad and the terminal pencil is shorter (5.5–10 mm; Figure 241b); it is indistinctly to sharply bi-coloured, brown-grey above and whitish to grey below. The paws are whitish to grey. Differences in colouration among subspecies are categorical in some cases (e.g. Feygin 1969).

The largest voles live in the Arctic tundra and in steppic habitats to the south-eastern Altai Mts., while those from the forest-steppe and mountain meadows of south-western Siberia are the smallest. The larger northern populations also grow faster (Dobrinskiy & Sosin 1981) and express a more pronounced secondary sexual dimorphism in size. The interorbital constriction is broadest relative to the length of the skull in voles from Altai and from the Arctic. Dupal (2000) recognised 4 groups of populations on the basis of skull size and proportions: (i) Polar tundra (long skull with wide interorbital region), (ii) south-eastern regions (long skull with narrow interorbital region), (iii) steppe and forest-steppe zones in Siberia (short skull with narrow interorbital region), and (iv) the Altai Mts. (short skull with wide interorbital region). Aksenova (1983) reported interpopulation variation in the length of the proximal baculum, which is 2.95 mm long in south-eastern Kazakhstan (Balkhash region) and 2.22 mm in Sakha.

From 10 to 16 subspecies have been proposed to categorise the geographic variation summarised above, but some authors have expressed concern as to whether all these subspecies are real (e.g. Gromov & Polyakov 1977). Due to the lack of a close match between the subspecies taxonomy and the phylogeographic structuring of *gregalis* (next paragraph), Pardiñas et al. (2017) refrained from recognising subspecies.

Genetically, *gregalis* consists of three phylogeographic lineages: B (the south-eastern margin of the range from western Tuva to Amur), C (a small range in Tuva), and a widespread A lineage occupying the rest of the range in the Arctic along the Lena River in the mountains of Central Asia and the steppe and forest-steppe zones to the west of Yenisei. Lineages B and C split ~0.24–0.45 Mya and are locally sympatric. The widespread lineage A is further structured into 6 sublineages which are largely allopatric and diverged at 0.2–0.3 Mya. The Arctic voles are in two sublineages, A2 and A5, encompassing the western (Yamal and NW Yakutia) and the eastern segments of the range, respectively; populations along the Lena River cluster with A5. Sublineage A1 contains voles from the forest-steppe zone from the southern Urals to Yenisei and the sublineage A6 includes samples from Kyrgyzstan and the Altai. Sublineages A3 and A4 cover the smallest and largely overlapping ranges in the Altai and vicinity and were found in sympatry (Petrova et al. 2015). The majority of the intraspecific diversity is therefore concentrated in the Altai Mts. and Tuva.

Figure 241: Tail in the common narrow-headed vole *Stenocranius gregalis* from the Yamal Peninsula, Russian Federation (a) and Tajikistan (b). Length of tail is 25 mm (a) and 28 mm (b), respectively.

All major forms of *gregalis* freely hybridise in captivity and the offspring are fertile (Gromov & Polyakov 1977). Hybrids between lineages A and B showed reduced viability (Koval'skaya 2015).

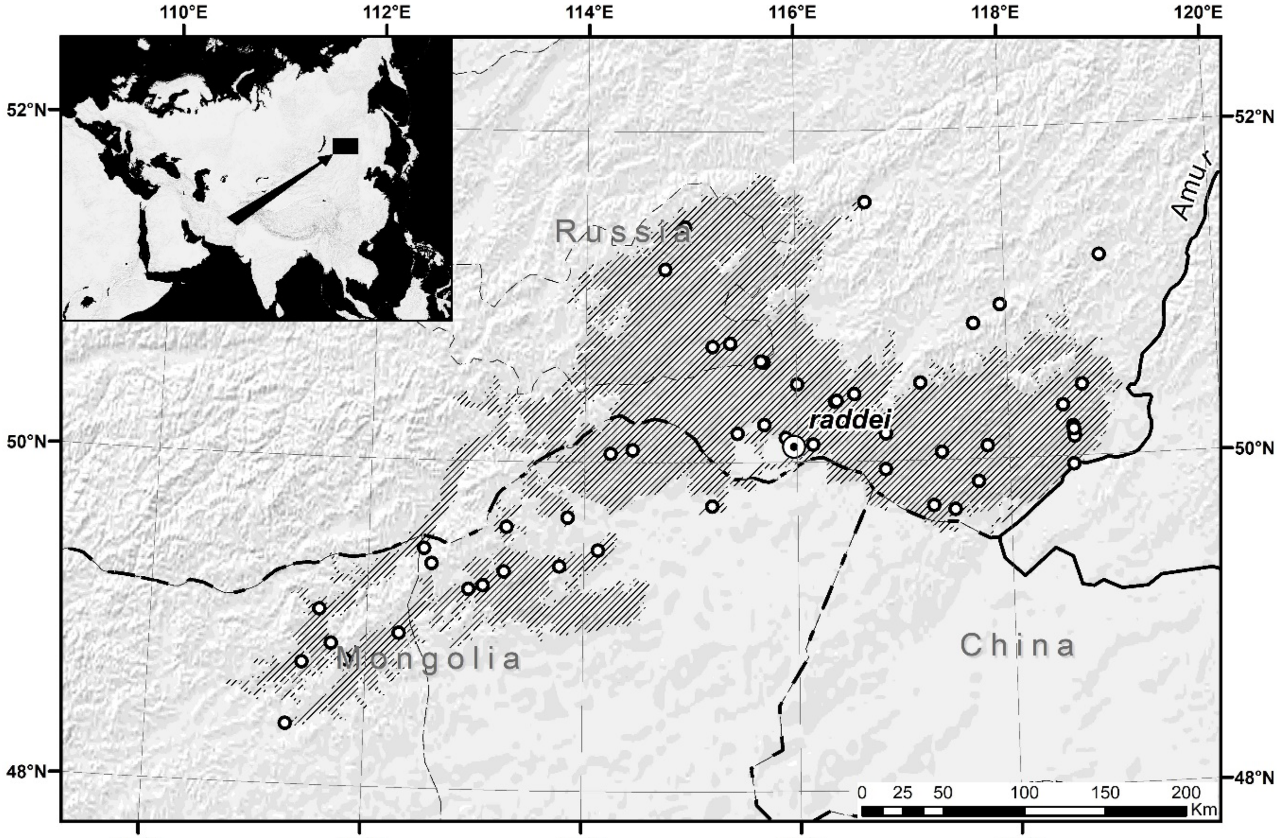


Figure 242: Distributional range of Radde's narrow-headed vole *Stenocranius raddei*.

Stenocranius raddei (Polyakov, 1881) – Radde's Narrow-headed Vole

Arvicola Raddei Polyakov, 1881:87. Type locality restricted by the lectotype to "L[ake] Tarey-Nor (Barun-Torey), s[outh]-e[ast] Transbaikalia" (Ognev 1950:485); now Barun-Torey, Zabaykalsky Krai, Russian Federation.

Taxonomy. Radde's narrow-headed vole was consistently treated as a subspecies in its own right although the scope was usually broader than understood here. Thus, Gromov & Polyakov (1977) included *angustus* into synonymy and Ognev (1950) added *kossogolicus*. Many authors defined *raddei* by its light buffy pelage (Kashkarov 1923, Allen 1940) which in the Transbaikal region indeed permits its separation from the darker *gregalis*. Radde's narrow-headed vole is believed to be a relic from the Early Pleistocene and retained the ancestral shape of M^3 (Petrova et al. 2016).

Distribution (Figure 242). Restricted to south-eastern Transbaikalia (Zabaykalsky Krai) of Russia and the districts of Dornod and Hentiy in adjacent Mongolia. The range is well-delimited by tributaries of the Amur: Ingoda and Shilka in the north and Ulidza and Argon in the south. The entire area is tentatively estimated at 58,100 km^2. Altitudinal range is 530–1,100 m.

Characteristics. Size and proportions are average. Dimensions: BWt=32–55 g, H&B=103–134 mm, TL=19–28 mm, HF=14.6–17.2 mm, EL=8–13 mm, CbL=23.9–28.3 mm, ZgW=12.1–14.5 mm, MxT=5.6–7.0 mm. Fur is soft and short. Dorsal side is buff to pale buff, grizzled and considerably lined with black. Mid-dorsal black stripe is most obvious on the frontal region and the neck but may extend as far back as the proximal lumbar region; the stripe is seen in ~25% of voles. The flanks are clearer buff and the transition is gradual. The ventral side is whitish and occasionally washed very pale buff. Hair bases are grey to slate while those on the chin are all-whitish. Feet are silver or buffy-white and the tail is uniformly whitish or indistinctly bi-coloured (grizzled black and buff above, whitish-grey below); terminal pencil is short (length=3.5–7.5 mm). Skull is very similar to the condition in *gregalis*; however, the antero-basilar part of the occipital bone and the bullae are wider (Figure 238). M_1 tends towards deeper re-entrant angles LR5 and BR4 than in *gregalis*; the variation is considerable. The M^3 is less complex with 3 inner salient angles; re-entrant angle LR4 is normally absent or very shallow. Karyotype in two voles from Soktuy-Milozan in Krasnokamenskiy Rayon (Chita region, Russia), reported as *Microtus gregalis raddei*, is identical to *gregalis*: 2n=36, NF_a=50 (Koval'skaya 1989).

Variation and subspecies. Monotypic. Genetic diversity of *raddei* is low (Petrova et al. 2015).

GENUS: *Microtus* Schrank, 1798 – Grey Voles

Taxonomy. *Microtus* is the central and most specious genus of arvicoline. During the last 50 years its scope was even wider, being tentatively identical to the current subtribe Microtina. Molecular phylogenetics (Jaarola et al. 2004, and subsequent papers) however narrowed the genus to a current ~60 species and 6 subgenera. The subgenera possibly diverged before the onset of the Pleistocene glaciations.

Distribution. From the Atlantic shores of Europe as far east as the mid-reaches of the Lena River and north-western Xinjiang; in the north, grey voles go beyond the Arctic Circle and reach northern Libya, southern Iran, and the mountains of Central Asia in the south. In the Nearctic Region, they are present from northern and Central North America as far south as Guatemala.

Characteristics. Size is small to large and the tail is shorter than ½ the head and body. There are 5–6 plantar pads. Females have 4–8 nipples; baculum is of standard trident type and distal digits are usually osseous. Zygomatic arches are usually widely expanded; the anteroconid complex of M_1 invariably consists of triangles T4–T5 and the anterior cap, but an additional pair of triangles (T6–T7) is frequently inserted behind the anterior cap. The sex chromosomes do not form a synaptonemal complex with X-Y pairing at pachytene (Borodin et al. 1995).

SUBGENUS: *Blanfordimys* Argyropulo, 1933

Taxonomy. The taxonomic scope of *Blanfordimys* follows *Mt*-DNA phylogenetic reconstruction (Bannikova et al. 2009) in which *afghanus* holds a basal position against *bucharensis* + *yuldaschi.* The idea that these species are closely related is not entirely new and already in the 1930s some Russian authors joined them under *Phaiomys* (e.g. Vinogradov 1933). Contemporaries more commonly classified *afghanus* and *bucharensis* as the only taxa in *Blanfordimys*, which was usually ranked as a subgenus of *Microtus* and only rarely as a genus in its own right (e.g. Ellerman 1941). Chaline (1974) synonymised *Blanfordimys* with *Neodon*, Corbet (1978) treated it as part of his broadly defined *Pitymys* while Zagorodnyuk (1991a) classified *afghanus* as the only extant species of *Allophaiomys*, a fossil genus with a time span 2.2–1.2 Mya (Martin & Tesakov 1998). The *yuldaschi,* on the other hand, was classified in *Phaiomys* or *Neodon* (a subgenera of *Microtus* or *Pitymys*). Kuznetsov (1965) regarded *yuldaschi* as part of *Lasiopodomys. Blanfordimys* is quite unique in some peculiarities of acoustic communication (Rutovskaya 2020) and is possibly a sister to *Euarvicola* (Bannikova et al. 2009, Steppan & Schenk 2017).

Distribution. Mountains and low hills between the south-eastern Caspian Sea and the ridges surrounding the Fergana valley, the eastern edge of Pamir and western Karakorum. The range covers south-eastern and southern Turkmenistan, north-eastern Iran, Afghanistan, southern Uzbekistan, Tajikistan, western Kyrgyzstan, and very marginally Kazakhstan, north-western China, and north-eastern Pakistan.

Characteristics. Moderately large and chunky voles with a large head and short tail (TL/H&B=0.22–0.40). There are 5 palmar and 6 plantar pads; the posterior sole from heel to the metatarsal pads is densely covered with stiff white hairs. Eyes are moderately large and semi-circular ears barely protrude above the fur. Hair is soft to silky. Pelage is usually light brown to greyish-buff above and the belly is whitish-grey to purely white. Baculum consists of a proximal stalk and a distal trident. The sperm head has a falciform acrosome; dimensions (length×width) are 6.90×2.80 µm in *afghanus* and 6.46×2.86 µm in *yuldaschi* (Aksenova 1978). Females have 8 nipples. The skull varies significantly; see under species. Enamel pattern is of a simple type; M^3 has a short posterior cap which incorporates T4; dental fields of T4–T5 on M_1 are confluent and the anterior cap is simple (Figure 243).

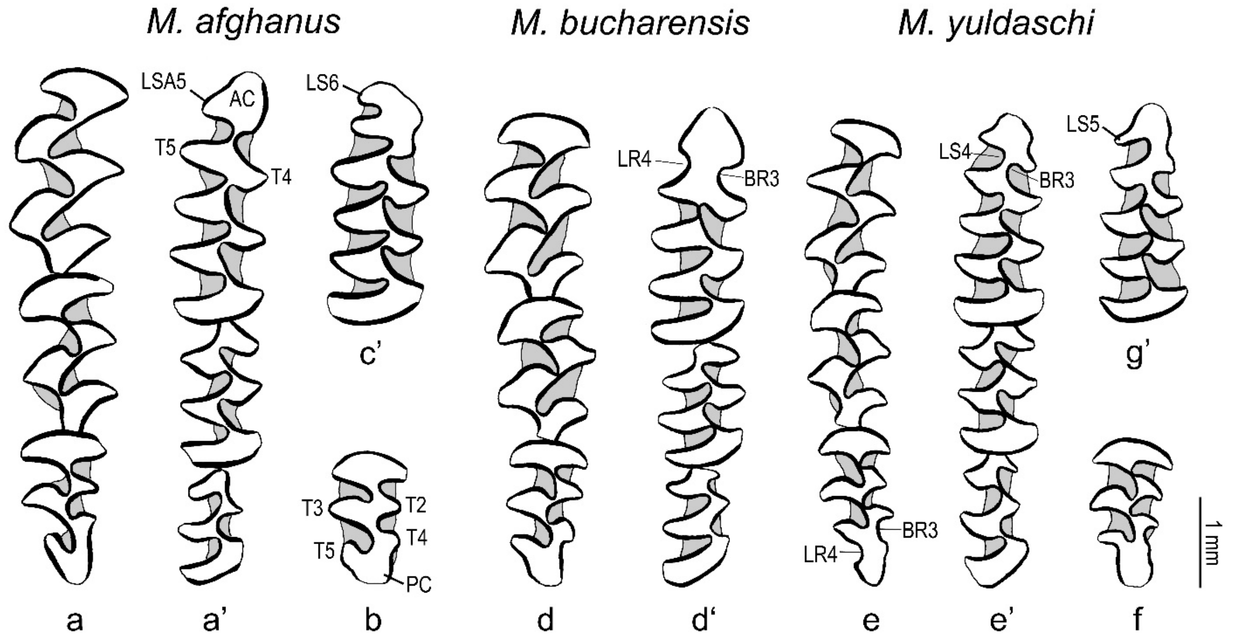


Figure 243: Molar pattern in voles from the subgenus *Blanfordimys*. *Microtus afghanus*: upper (a) and lower row (a'–Salang Pass, Baghian, Afghanistan); isolated M^3 (b–Badkhis, Turkmenistan) and M_1 (c'–Kulyab, Khatlon, Tajikistan). *M. bucharensis*: upper (d) and lower row (d'–Pendzhikent, Sughd Region, Tajikistan). *M. yuldaschi*: upper (e) and lower row (e'–Gissar Range, Tajikistan); isolated M^3 (f–Obipitoudu, Khatlon Province, Tajikistan); isolated M_1 (g'–Bulunkul', Gorno-Badakshan, Tajikistan).

Key to species

1a) Tail sharply bi-coloured; baculum: central digit >½ the length of the proximal baculum; bullae and the mastoid portion of temporal of normal size; supratemporal ridges well developed and normally fuse into sagittal crest in old individuals; M^3 frequently with long PC and feeble salient angles LS5 and BS4 …………………………………..…...………….. *yuldaschi*

1b) Tail indistinctly bi-coloured or uniformly light; baculum: central digit <½ the length of the proximal baculum; bullae and the mastoid portion of temporal greatly enlarged; supratemporal ridges absent or weakly developed, there is no sagittal crest; M^3 with short and simple PC and with no salient angles LS4 and BS4 ……………………………………….……………….. 2

2a) Baculum with a narrow base (width=1.10–1.40 mm); bullae smaller, usually extending till the level of the occipital condyles or slightly beyond; incisive foramina shorter, not reaching the level of M^1; M_1 usually with deep re-entrant angles BR3 and LR4, separating AC from triangles T4–T5; 2n=58 ………………………………………………. *afghanus*

2b) Baculum with a wide base (width=1.35–1.73 mm); bullae larger, extending well beyond the level of the occipital condyles; incisive foramina longer, reaching the level of M^1; M_1 with shallow re-entrant angles BR3 and LR4; as a result the dental fields of AC and triangles T4–T5 are widely confluent; 2n=48 ………………………………………………. *bucharensis*

Microtus afghanus Thomas, 1912 – Afghan Vole

Taxonomy. The species distinction of *afghanus* was never questioned. The type specimen was collected as early as 1843 but quite astonishingly was first misidentified as "A variety or distinct species" *Golunda [Millardia] meltada,* Muridae (Horsfield 1851:144) and afterwards as *Arvicola [Lasiopodomys] mandarinus* (Blanford 1881b:108, Thomas 1889:59).

In the past, *afghanus* contained *bucharensis* as a subspecies; the two voles are not in a sister position. Interspecific hybridisation yielded a high mortality in gravid females, frequent abortions, a high mortality of offspring and their sterility. On the other hand, intra- and inter-subspecific hybrids in *afghanus* showed no differences in reproductive parameters, including offspring mortality and fertility (Golenishchev & Sablina 1991).

Distribution (Figure 244) area of 109,940 km^2 largely coincides with the north-eastern edge of the Iranian Plateau. The range is in 3 fragments; each consists of a number of isolated patches of different size. The first

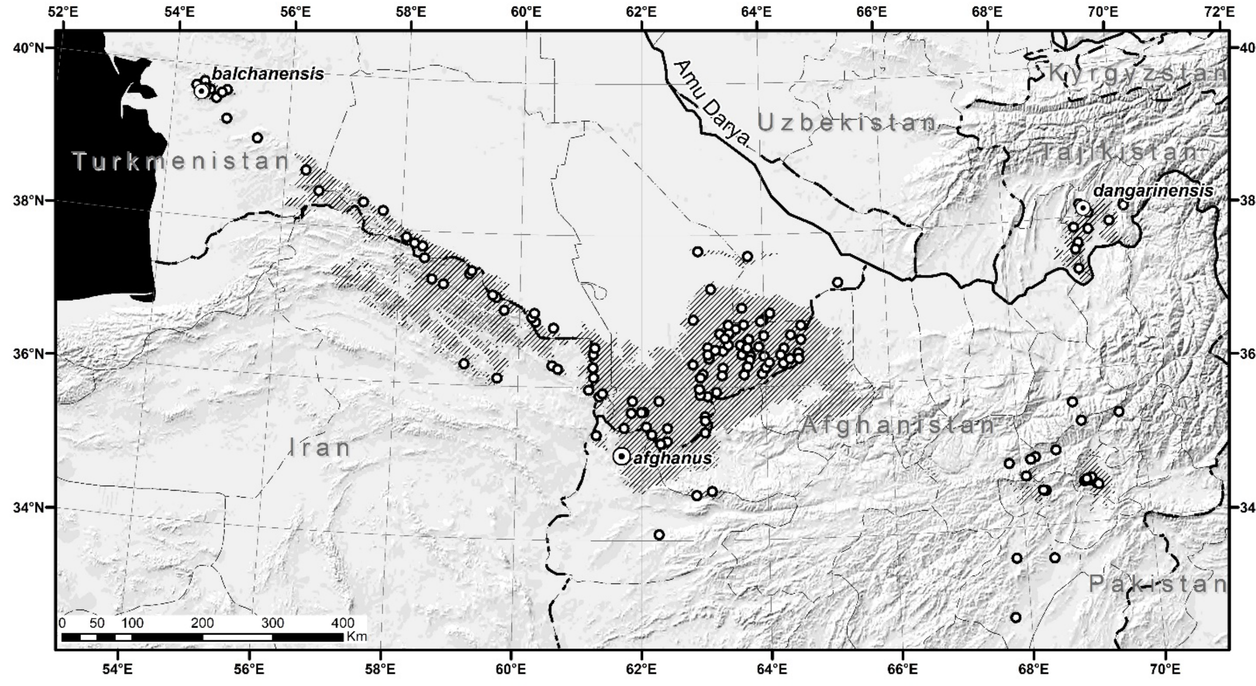


Figure 244: Distributional range of the Afghan vole *Microtus afghanus*.

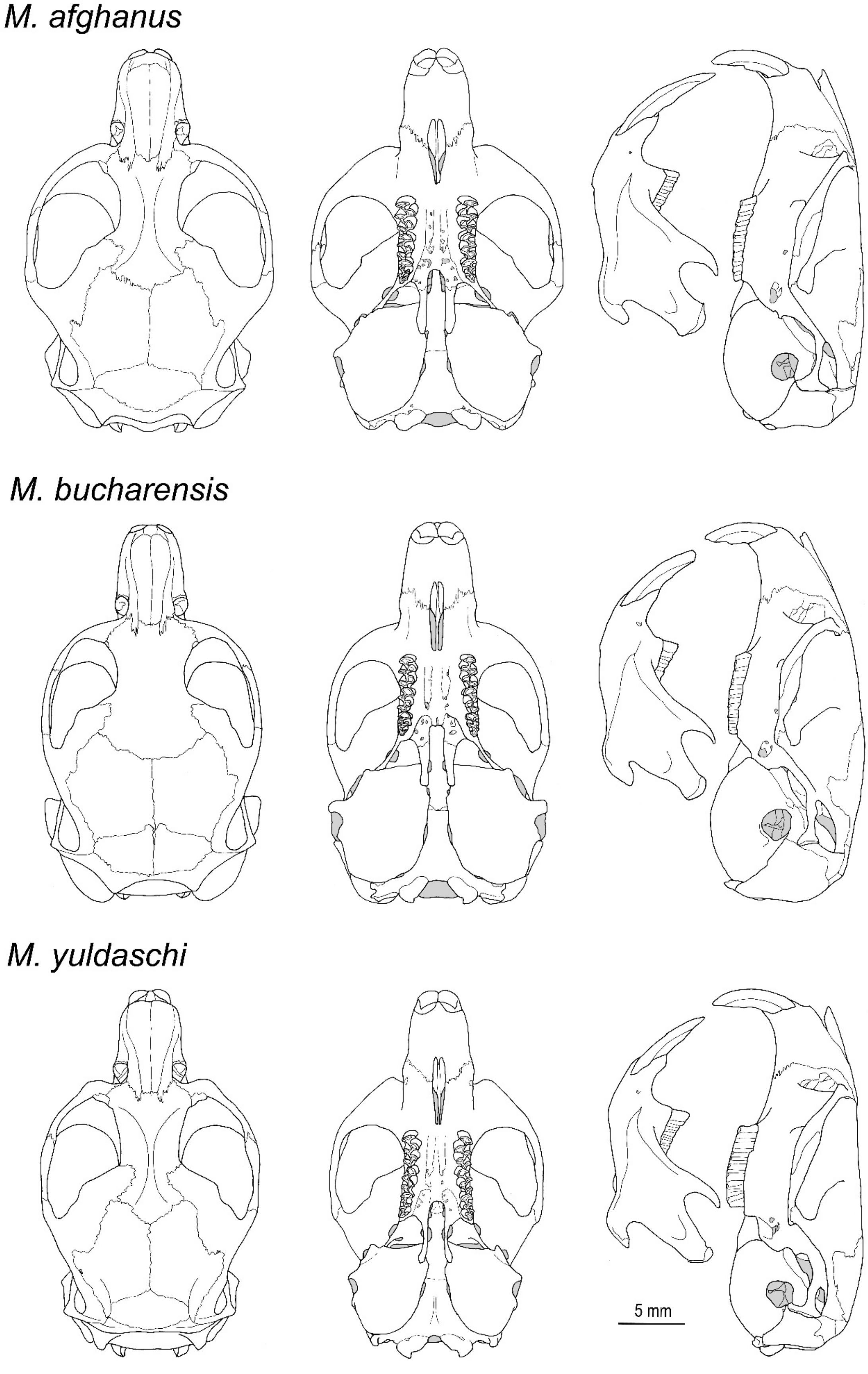


Figure 245: Skull in voles from the subgenus *Blanfordimys* (top to bottom): *Microtus afghanus* (top–near Kabul, Afghanistan), *M. bucharensis* (middle–Zebon, Sughd Province, Tajikistan), *M. yuldaschi* (bottom–Kara-Kul' Lake, eastern Pamir Mts. Tajikistan).

fragment, containing 6 large isolates (each >100 km^2) and 6 smaller patches, is in the Bol'shoy Balkhan (near the south-eastern Caspian coast in Turkmenistan), Kopet Dag Mts. (both sides of the Turkmen-Iranian border), in north-western Hindu Kush (Badghis and Herat in northern Afghanistan and south-eastern Turkmenistan) and the transitional area towards the Karakum. The next fragment contains 3 large and 10 small isolates and centres on the Kūh-e Bāba Mts. (Hindu Kush) in eastern Afghanistan (provinces of Baghlan, Bamiyan, Ghazni, Kabul, Panjshir, Parwan, and Wardak). The north-eastern fragment (2 large and 1 small isolates) is the smallest and occupies south-western Tajikistan to the east of the Vakhsh River. The Afghan vole prefers a dense turf of grasses and herbs on clay and loess soils, from semi-deserts to the mountain pastures; winters are usually rainy and snowy and the micro-habitat retains humidity for most of the year. The Afghan vole seeks humid depressions and is generally common along watercourses (Hassinger 1973, Siahsarvie et al. 2005). The altitudinal range is 200–3,550 m.

Characteristics. Tail is short (TL/H&B=0.22–0.30) and well-furred, hence the annulation is nearly concealed; terminal pencil is ~3–5 mm long. Hair (length ~8–10 mm) is soft to silky. Dorsal side is pinkish-buff to brown, clear on flanks and thighs but dorsally grizzled by blackish-brown tips of the longer hairs; underparts white and clouded with slate underfur. Ears are grey, occasionally shaded buff, paws light buff to whitish-cream, tail greyish-buff or greyish-cream, indistinctly bi-coloured (darker above), clearly darkened towards the tip in some individuals. The proximal baculum is 2.35–2.65 mm long and 1.10–1.40 mm wide; length of distal digits is 0.85–1.30 mm (central digit) and 0.70–1.05 mm (lateral digits; Aksenova 1983). Skull is deep and slightly bowed in dorsal profile. Zygomatic arches are well-expanded (ZgW/CbL=0.57–0.64), interorbital region is wide and the large bullae (length of bullae/CbL=0.31–0.35) usually reach the level of the occipital condyles or project slightly beyond (Figure 245). Incisive foramina short, not reaching the plane of M^1. Mastoids inflated; temporal ridges weak and present late in life. Alveolar process is prominent (Figure 246a). The M^3 is simple with 2 triangles which alternate or are widely connected (Figure 243a,b). The posterior cap is short and simple and the posterior re-entrant angles are weak; the LR4 is not present at all. M$_1$ has anterior triangles T4–T5 broadly confluent and usually isolated from the anterior cap. Karyotype: 2n=58, NF$_a$=56; the X is submetacentric and all the remaining chromosomes are acrocentric (Golenishchev & Sablina 1991).

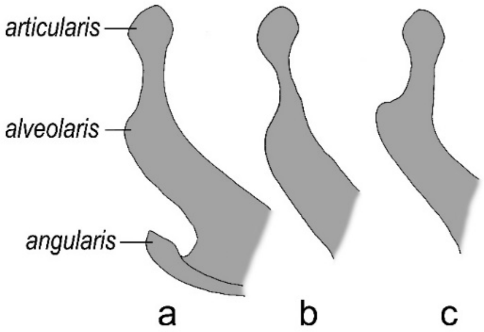


Figure 246: Caudal view of ramus mandibulae in voles from the subgenus *Blanfordimys*: a–*Microtus afghanus* (near Kabul, Afghanistan), b–*M. bucharensis* (Pendzhikent, Sughd Region, Tajikistan), c–*M. yuldaschi* (Bulunkul', Gorno-Badakshan, Tajikistan). The processes are indicated.

Variation and subspecies. Three weakly defined subspecies are usually recognised.

Microtus afghanus afghanus Thomas, 1912

Microtus (Phaiomys) afghanus Thomas, 1912a:349. Type locality: "Gulran", geo-referenced as "about 35° N., 62° E., Afghanistan" (Ellerman & Morrison-Scott 1951:681).

Distribution. Turkmenistan (except the Bol'shoy Balkhash), north-eastern Iran and Afghanistan.

Characteristics. Larger with yellowish pelage. Dimensions: BWt=24–54 g, H&B=90–121 mm, TL=15–30 mm, HF=15–19 mm, EL=8–13 mm, CbL=24.0–28.7 mm, ZgW=14.0–17.9 mm, MxT=5.6–7.2 mm. Dorsal side is light dull buff. The inner salient angle LS6 is rarely present on the anterior loop of M^1. Interorbital width varies with altitude; in Afghanistan, the mean is low ($\bar{x}$=4.11 mm) above 2,500m, and high ($\bar{x}$=4.38 mm) below 2,200 m (Niethammer 1970a).

Microtus afghanus balchanensis Heptner & Shukurov, 1950

Microtus afghanus balchanensis Heptner & Shukurov, 1950:149. Type locality: "spring Kendyrli, northern slope of Bol'shie Balkhany [Mt. Bol'shoy Balkhan] (1000 m above sea level). Western Turkmeniya [Turkmenistan]."

Distribution. Mt. Bol'shoy Balkhan, south-western Turkmenistan (Golenishchev & Sablina 1991).

Characteristics. Dimensions: BWt=28.5–50 g, H&B=91–110 mm, TL=23–28 mm, HF=16–18.6 mm, EL=8–11 mm, CbL=25.3–27.0 mm, ZgW=14.3–15.6 mm, MxT=5.5–6.5 mm. A dark subspecies: dorsal fur washed brown, flanks yellow. The anterior loop of M^1 rarely with the inner salient angle LS6.

Microtus afghanus dangarinensis Golenishchev & Sablina, 1991

M[icrotus] a[fghanus] dangarinensis Golenishchev & Sablina, 1991:107. Type locality: "Dangarinskiy rayon in Tajik SSR [Tajikistan]."

Distribution. South-western Tadjikistan to the east of the Vakhsh River in the southern edges of the Vakhskiy mountain ridges (Karatau), and in the south-eastern foothills of Khazratishokh.

Characteristics. Dimensions: BWt=26–42 g, H&B=94–110 mm, TL=24–29 mm, HF=15–16.8 mm, EL=8–10.3 mm, CbL=25.0–27.7 mm, ZgW=14.7–16.4 mm, MxT=6.1–7.0 mm. Colouration as in *balchanensis*. The anterior loop of M^1 frequently with an additional inner salient angle LS6 (Figure 243c').

Microtus bucharensis Vinogradov, 1930 – Bucharian Vole

Distribution (Figure 247). The range covers 26,120 km^2 in deserts, piedmont semi-deserts and mountains (altitude=65–1,900 m) in southern Uzbekistan (regions of Jizzakh, Qashqadaryo, Samarqand, and Surxondaryo; with an isolate in Navoly); western Tajikistan (Karategin, Khatlon, and Sughd), and very marginally south-eastern Turkmenistan (Lebap: Kugitang Mts.). Lives in meadows with dense vegetation and abandoned fields.

Characteristics. Externally similar to *afghanus* with a slightly longer tail (TL/H&B=0.25–0.33) and longer fur (10–11.5 mm). The tail is rather sparsely covered by hair and the underlying annulation is visible; terminal pencil is short (1.2–2 mm). Dorsal fur is greyish-buff, shaded rusty in some animals, flanks are uniformly buff and the belly is whitish to purely white, but heavily clouded by slate underhair. Ears are longer than the fur, greyish-buff; the paws are light-buff and the tail is nearly uniformly light greyish-buff. Baculum has a narrow base (width=1.35–1.75 mm); the length of the main stalk is 2.53–2.63 mm, and the length of the distal digits is 1.03–1.10 mm (the central digit) and 0.85–0.95 mm (lateral digits; Golenishchev & Sablina 1991). Skull is deep (height behind M^3/CbL=0.34–0.35) with well-expanded zygomatic arches (ZgW/CbL=0.56–0.62), a wide interorbital region (wider than in *afghanus*), and very large bullae (length of bullae/CbL=0.33–0.38) projecting beyond the plane of the occipital condyles. Mastoids are extremely inflated. The dorsal profile is bowed, reaching the highest point at the fronto-parietal suture. Incisive foramina are longer than in *afghanus*, posteriorly nearly reaching the level of M^1 (Figure 245). Mandible is without peculiarities; the alveolar process is the weakest in the subgenus (Figure 249b). M1 has shallow anterior re-entrant angles LR4 and BR3, hence triangles T4–T5 are confluent with the anterior cap (Figure 243d'). Karyotype: 2n=48, NF_a=50; except for 2 pairs (a large subtelocentric and a small metacentric), all the remaining autosomes and both heterosomes are acrocentric (Golenishchev & Sablina 1991).

Variation and subspecies. Two weakly defined subspecies are usually recognised.

Microtus bucharensis bucharensis Vinogradov, 1930

M[*icrotus*] (Phaiomys) *bucharensis* Vinogradov, 1930:45. Type locality restricted by lectotype (Vinogradov 1931:13) to "Zeravshankette, 8 km south of Pendzhakent, near Kischlak Sivon [village Zivan or Zebon)], 2200 m", 8 km south of Pendzhikent, Zeravshankiy ridge, Tajikistan.

Synonyms. *Microtus bucharicus* Vinogradov, 1931 [absolute synonym of *bucharensis*].

Distribution. Zeravshan and Turkestan mountain ridges of north-western Tajikistan (Sughd Region) and south-western Uzbekistan (Jizzax, Samarqand, and Qashqadaryo Regions), Baysuntau ridge in south-western Uzbekistan (Surxondaryo Region) and the Kugitang Mts. in south-eastern Turkmenistan (Lebap Region). Smaller isolates are also in the Nuratau Mts. (Jizzax, Samarqand and Navoiy Regions in Uzbekistan), Tamdytau and Kuldzhuktau Mts. (Navoiy Region in Uzbekistan) and Mt. Mogoltau (Sughd Region in south-western Tajikistan).

Characteristics. Dorsal pelage light with buff tints. Dimensions: BWt=28–32 g, H&B=91–115 mm, TL=26–37 mm, HF=16–18 mm, EL=9–12 mm, CbL=25.5–29.5 mm, ZgW=15.2–17.5 mm, MxT=6.4–7.1 mm.

Microtus bucharensis davydovi Golenishchev & Sablina, 1991

M[icrotus] b[ucharensis] davydovi Golenishchev & Sablina 1991:109. Type locality: "Tajik SSR [Tajikistan] in district of Shakhrinau, kishlak Tashakhur."

Distribution. Mountain ridges (Babatag, Oktau, Aruktau, Karatau) in south-western Tajikistan between the Surkhan-Darya and Vakhsh Rivers (south-western Karategin and north-western Khatlon Regions).

Characteristics. Dorsal pelage duller and greyer than in the nominal subspecies. Dimensions: H&B=90–127 mm, TL=21–34 mm, HF=15.5–19.8 mm, EL=9.2–13.2 mm, CbL=27.3–30.0 mm, ZgW=15.6–18.0 mm, MxT=6.4–7.0 mm.

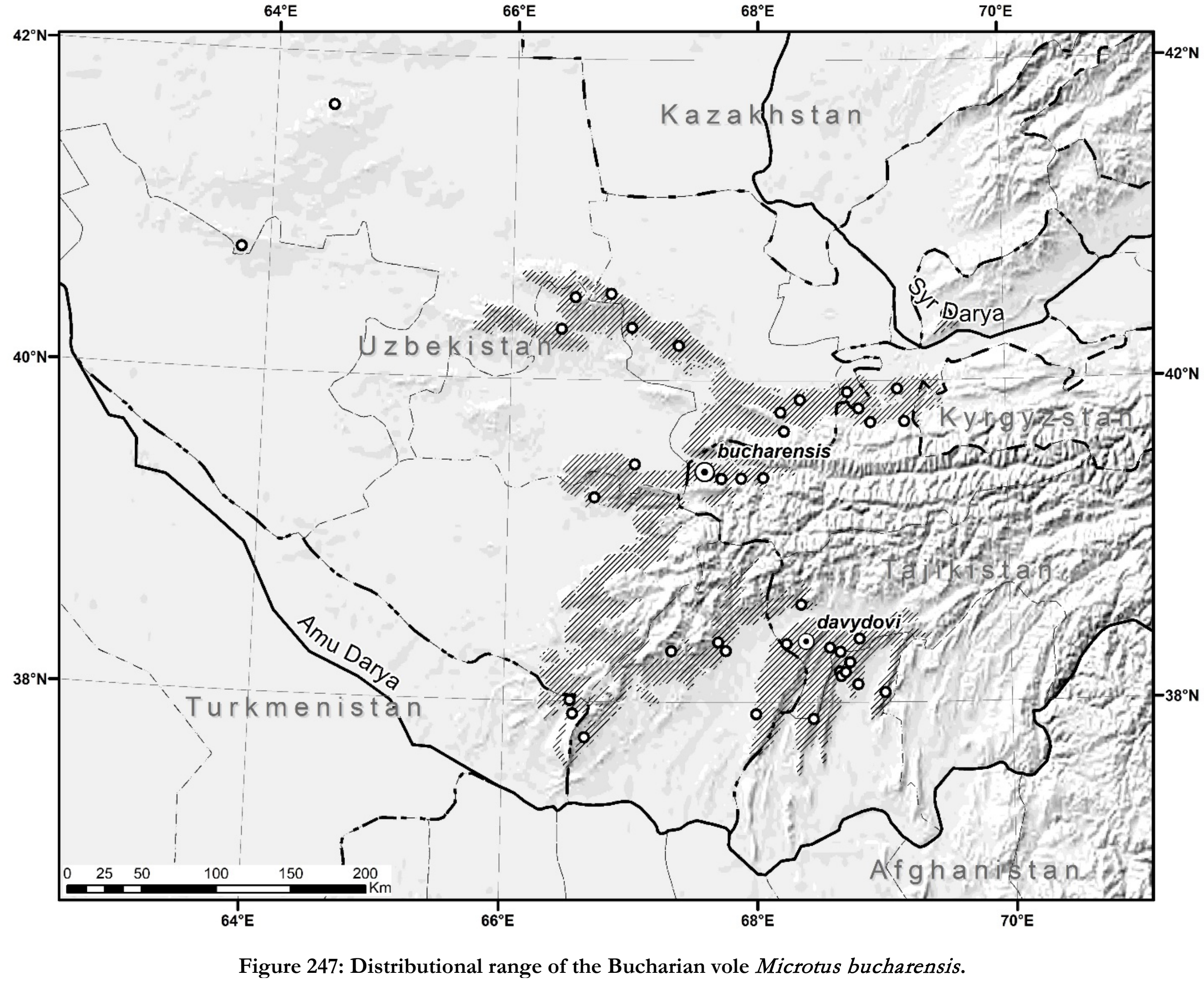


Figure 247: Distributional range of the Bucharian vole *Microtus bucharensis*.

Microtus yuldaschi (Severtsov, 1879) – Juniper Vole

Nomenclature. Juniper vole is at present known by the species name *juldaschi*, the original spelling however was *yuldaschi* (Severtsov 1879). Pavlinov et al. (1995:110) highlighted the inconsistent spelling, presuming that *yuldaschi* was emended to *juldaschi* at one point but they were unable to trace the source. Musser & Carleton (2005:879) agreed about the original spelling and concluded that the "alteration to *juldaschi* [is] unclear". So far, Baranova & Gromov (2003:84) have been the only authors to use Severtsov's original spelling.

Evidently, *juldaschi* was an unintentional change (lapsus calami) of *yuldaschi* which entered general use during the 1930s. Severtsov's (1879) description appeared in Russian in a journal largely unavailable outside Russia. For example, seven decades after Severtsov's (1879) description of *yuldaschi,* the publication was still not available in the Library of the British Museum (Natural History) in London (Ellerman & Morrison-Scott 1951:683). Unsurprisingly, western authors missed the name from the start (e.g. Blanford 1881b, Hinton 1923), and Miller (1899a) and Thomas (1909b) independently named the same species *pamirensis* and *carruthersi*, respectively. Even among Russian mammalogists there was a poor understanding of the juniper vole at the turn of the 19th century. A decade after Severtsov's paper, the Zoological Museum of the Moscow University still did not possess a single voucher (Tikhomirov & Korchagin 1889) and the first were collected in summer 1936 (by Shchukin; Ognev's collection in Moscow). We were unable to find a single publication using the name *yuldaschi* prior to Vinogradov's 1930 paper, where it was already spelled *juldaschi.* Boris S. Vinogradov (1891–1959), a prominent Russian mammalogist of the Soviet era, was appointed curator of mammals in the Zoological Institute in Leningrad [St. Petersburg] in 1921 (Gromov 1982) and developed an interest in Central Asiatic rodents in 1930. Although an indisputable authority on the taxonomy and morphology of Palaearctic rodents, he was superficial in

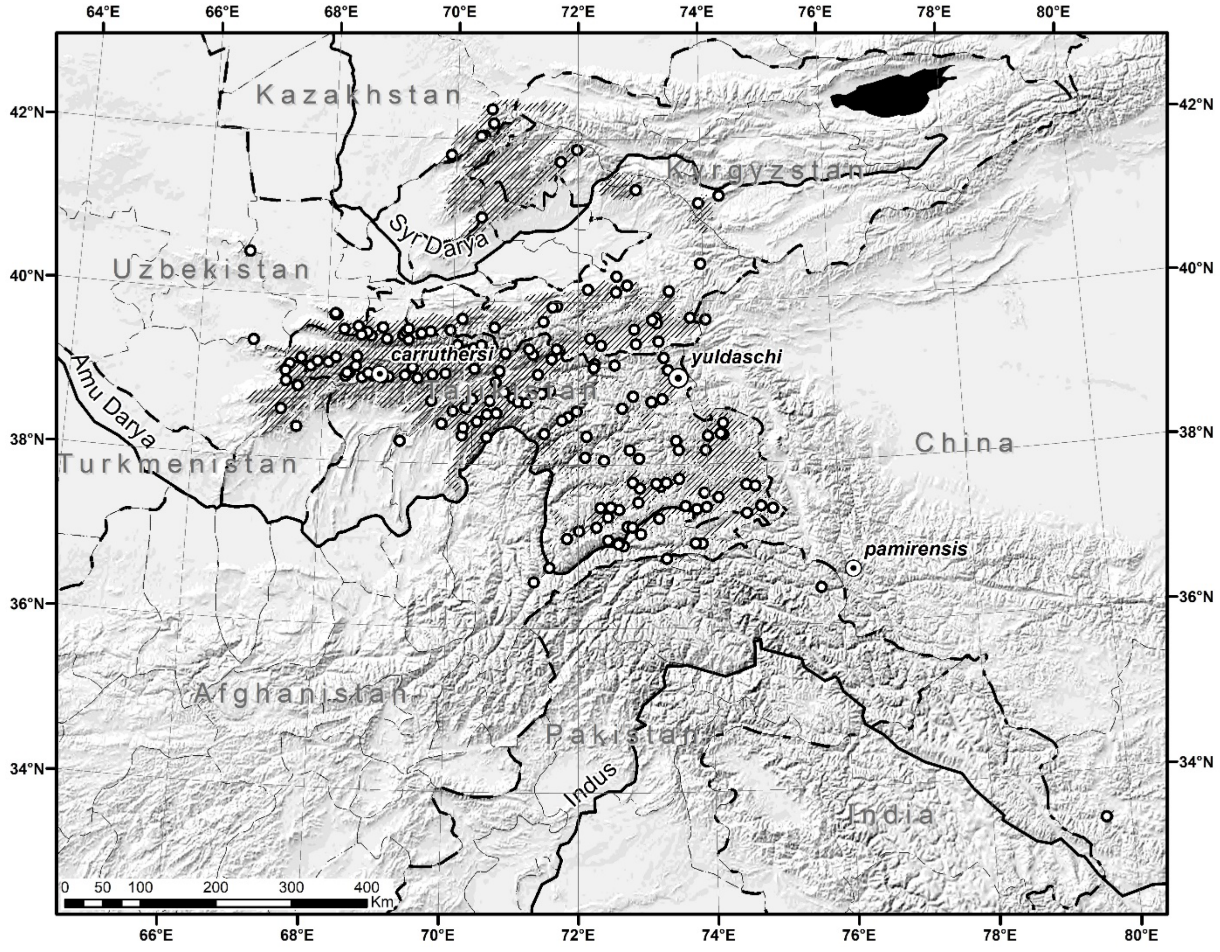


Figure 248: Distributional range of the juniper vole *Microtus yuldaschi*.

his treatment of nomenclatural issues. Our review of names for Palearctic arvicolines uncovered Vinogradov's incorrect subsequent spelling in over 20 genus- and species-group names, including a further two errors in *yuldaschi* itself: *juldashi* and *julaaschi*. Spelling of *yuldaschi* as *juldaschi* in Vinogradov (1930) was evidently an unintentional change which escaped notice for 55 years. In accordance with the Code, the original spelling *yuldaschi* is to be preserved unaltered (Art. 32.3) and should replace the incorrect spelling *juldaschi*.

Distribution (Figure 248). The range expands over 97.650 km^2 in south-eastern Uzbekistan (regions of Qashqadaryo, Samarqand, Surxondaryo, and Toshkent), Tajikistan (except for the south-western Khatlon Region), and western Kyrgyzstan (Batken, Jalal-Abad, and Osh); marginally present in Chimkent in Kazakhstan, north-western Afghanistan (Badakhshan), northern Pakistan (Northern Areas and the North-West Frontier), and north-western China (Xinjiang and Xizang). The juniper vole occupies meadows with short (5–15 cm) grass and scrubs at high elevations (1,530–4,730 m, mainly >2,200–3,750 m a.s.l.) in the ranges of the Pamir, Pamir-Alay and Tien Shan. An isolate is in the Nuratau ridge and very marginally the Karakoram. These voles show morpho-physiological adaptations towards burrowing (Bol'shakov et al. 1975a) and avoid rocky habitats.

Characteristics. A vole of moderate size and comparatively short tail (TL/H&B=0.25–0.40). Fur is long (8.5–12 mm; protruding hairs 10–14 mm), soft and fine. Dorsal pelage is uniformly pinkish-buff, pale brown, brown or greyish-brown; underside is whitish or greyish, over-shaded with slate bases and occasionally with a buffy tint. Flanks are light-buff in some animals, the demarcation is rather distinct. Ears are greyish and paws are whitish. The tail is indistinctly bi-coloured, ochre or brown above, greyish-white below; the terminal pencil is short (3–5.5 mm). Baculum consists of a robust proximal bone (length=2.15–2.75 mm; width =1.10–1.75 mm), a comparatively long (1.20–1.70 mm) and bulky central digit, and short (0.60-1.00 mm) lateral digits. In comparison with *afghanus* and *bucharensis*, *yuldaschi* has a proportionally longer distal baculum and a categorically more robust proximal stalk (Aksenova 1983). Skull has a comparatively longer braincase on less expanded zygomatic arches (ZgW/CbL=0.53–0.60) and weak temporal ridges which frequently merge into a shallow sagittal crest. Nasals are bottle-shaped, incisive foramina are long, bullae are comparatively small, and the mastoid portion of the temporal is of normal size (Figure 245). The alveolar process on the mandible is more prominent than in either *afghanus* or *bucharensis* (Figure 246c). Molars are the most complex in the subgenus; posterior cap on M^3 is normally longer and with distinct posterior re-entrant angles BR3 and LR4. On M^1, re-entrant angles BR3 and LR4 are deep and frequently isolate the anterior cap from the triangles T4–5 (Figure 243e,f). Furthermore, deep LS3 isolates T4 in some animals. Karyotype: 2n=54; the X is large acrocentric or metacentric and the Y is small acrocentric. Four cytotypes are known, differing in number of chromosomal arms (NF_a=52–58) due to 3–4 pericentric inversions (Gileva et al. 1982); see under subspecies. Karyotype does not show close affinities between *yuldaschii* and *afghanus* (Agadzhanyan & Yatsenko 1984).

Variation and subspecies. Two allopatric taxa of juniper voles (*yuldaschi* and *carruthersi*) were recognised throughout the 20th century and were ranked as distinct species for a considerable time (Vinogradov 1930, Ognev 1950, Ellerman & Morrison-Scott 1951). In cross-breeding trials various populations of *yuldaschi* and *carruthersi* produced fertile offspring (Bol'shakov et al. 1975b); the only exceptions were F1 male hybrids produced by the Tallaskiy population which were sterile (Gileva et al. 1982). These taxa are uniformly ranked as distinct subspecies (Shenbrot & Krasnov 2005, Pardiñas et al. 2017).

Microtus yuldaschi yuldaschi (Severtsov, 1879)

Arvicola Yuldaschi Severtsov, 1879:63. Syntypes were from "Pamir, […] Karakul' and near Aksu". Lectotype fixation (Vinogradov 1931:12) restricted the type locality to "(Lake) Karakul', Pamir (Gorniy Badakshan [Kuhistoni Badakhshon], Tajikistan" (Baranova & Gromov 2003:84).

Synonyms. *Microtus pamirensis* Miller, 1899.

Distribution. Pamir, Alay Valley and western Karakorum in eastern Tajikistan, south-western Kyrgyzstan, north-eastern Afghanistan, north-western Pakistan, and western China.

Characteristic. Larger: BWt=14–36 g, H&B=90–125 mm, TL=20–41 mm, HF=13.8–18 mm, EL=10–15 mm, CbL=23.5–27.8 mm, ZgW=13.4–16.4 mm, MxT=5.7–6.8 mm. Skull is more ridged and angular, the sagittal crest prominent. Baculum is on average longer (proximal bone=2.63 mm, distal digit=1.53 mm, lateral digit=0.90 mm) with narrower basal expansion (1.55 mm; Aksenova 1983). Karyotype: NF_a=52–54; the X is metacentric (Gileva et al. 1982).

Microtus yuldaschi carruthersi Thomas, 1909

Microtus (Pitymys) carruthersi Thomas, 1909b:263. Type locality: "Hissar Mountains, 100 miles [160 km] E. of Samarkand, 9000–10,000' [2,745–3,050 m]", Tajikistan.

Distribution. Pamiro-Alay and western Tien Shan in eastern Uzbekistan, western Tajikistan, north-western Kyrgyzstan and Kazakhstan.

Characteristic. Smaller: BWt=14–33 g, H&B=80–117 mm, TL=24–50 mm, HF=12–17.7 mm, EL=10.5–15 mm, CbL=23.4–26.1 mm, ZgW=13.1–15.5 mm, MxT=5.7–6.8 mm. Skull smoother, temporal ridges rarely fuse to form the sagittal crest. Baculum is on average shorter (proximal bone=2.41 mm, distal digit=1.32 mm, lateral digit=0.68 mm) with broader basal expansion (1.29 mm; Aksenova 1983). Karyotype: NF_a=52 (all autosomes acrocentric; Tallaskiy Alatau), 54–56 (Gissarskiy Ridge), or 56–58 (Turkestanskiy Ridge); both heterosomes are acrocentric (Gileva et al. 1982).

SUBGENUS: *Euarvicola* Acloque, 1900 – Field Voles

Euarvicola Acloque, 1900:49. Type species by monotypy: *[Hemiotomys] agrestis* Linné. The year of publication is usually quoted as 1899 (Miller 1912a:659, Ellerman & Morrison-Scott 1951:690, Pavlinov & Rossolimo 1987:190, etc.). Acloque dated the preface to his book as 31 Decembre 1899 (p. vi), and 1900 is printed on the title page.

Synonyms. *Agricola* J. H. Blasius, 1857 [preoccupied by Bonaparte 1854, for Aves]; *Sylvicola* Fatio, 1867 [synonymous with *Agricola* Blasius and preoccupied by Harris 1776, for Insecta].

Taxonomy. Miller saw the differences between *M. arvalis* and *agrestis* as being "too slight to entitle the groups to rank as distinct subgenera" (Miller 1896:17) and classified both into subgenus *Microtus* where it remained for most of the 20th century. Towards the end of the century, *agrestis* was transferred into *Agricola* which was commonly ranked as a subgenus (e.g. Zagorodnyuk 1990) or rarely as a genus (Lissovsky et al. 2019). Miller (1896) stressed that *Agricola* is a preoccupied name, hence the oldest available name for field voles at the genus-group level is *Euarvicola*.

Over the last two decades various phylogenetic reconstructions stressed the erratic placement of the *agrestis*-group and its unresolved position against other voles. Fink et al. (2010) suggested that the origin of the *agrestis* lineage may be a hint of the first *Microtus* radiation in Europe. Several authors proposed a sister position of *agrestis* with respect to *Blanfordimys* (Jaarola et al. 2004) and Robovský et al. (2008) advocated for the monophyly of the *agrestis-Lasiopodomys-Blanfordimys* clade. Barbosa et al. (2018) suggested a sister position of *agrestis* and *cabrerae* and their placement in a subgenus *Agricola.*

Trouessart (1897, 1910) and Miller (1912a) recognised a single species of field vole (i.e. *agrestis*) and this view was nearly universally adopted throughout the 20th century. This belief was shaken by molecular phylogenetic reconstructions (Jaarola & Searle 2002, Paupério et al. 2012) which led to a taxonomic split into the current 3 species (Pardiñas et al. 2017). These species are very similar morphologically, share almost identical karyotypes, and are largely allopatric. They show substantial genome-wide differentiation, divergence at the *Cytb* of up to 6%, and are reciprocally monophyletic. Little evidence of gene flow among these species was found (Fletcher et al. 2019) which speaks to their taxonomic distinctness.

Distribution. A wide Palaearctic range from the Atlantic coast till the mid-reaches of the Lena River and north-western Xinjiang; the latitudinal range is wide in Europe, from the northern coasts as far south as the Mediterranean Sea; absent from the majority of southern peninsulas and from arid steppes and semideserts further east. To the east of the Urals, the range is narrowed to the taiga belt.

Characteristics. (Figure 249). Form and appearance are typical for the genus. Tail is short (TL/H&B~0.35), its annulation shows through the hair; the terminal tuft is distinct. There are 5 palmar and 6 plantar pads; their configuration is similar as in *Microtus* s.str., except for the medial metatcarpal pad which is decidedly larger in *Euarvicola* (Figure 250a'). The minute thumb is nearly concealed dorsally by a relatively large nail. The ears are evenly rounded and hidden in the fur; the meatal lobe is well developed but not different from *Microtus* s.str.; the hairs inserted at the base of the ear are characteristically long and protrude over it (cf. Dienske 1969). The antihelix is covered by long and fluffy hairs which are short in *Microtus* s.str. (Figure 251). The eyes lie nearer the muzzle than the ear base. The fur is thick but varies in texture from soft to coarser, giving the animal either a sleek or shaggy appearance; the longer hairs of the back reach ~15 mm in winter; ordinary hairs are ~12 mm long. Back is clear brown or greyish-brown; the spine and rump are frequently darkened by abundant long dusky hairs. The underside is silvery and can sharply contrast the brown flanks; the slaty hair bases are frequently visible; the tail is bi-coloured. Females have 8 nipples; the baculum is of trident shape but the lateral digits are small. Skull is essentially as in *Microtus* s.str.; zygomatic arches are moderately expanded (ZgW/CbL=0.54–0.61) and nasals are short (<⅓ the skull length); postorbital processes are of modest size (Figure 252). Posterior palate shows a short, broad and low medial crest. Mandibular foramen is situated over the protuberance of the lower incisor and close to the posterior margin of *ramus mandibulae* (closer to its anterior margin in *Microtus* s.str.; Fig. 260). Molars are highly characteristic, having an additional postero-lingual salient angle LS4 (=T5) on a variable proportion of M^1 specimens and on >95% of M^2; the dental field of T5 is usually isolated on both molars (Figure 253). M^3 nearly always has 4 inner and 3 outer salient angles and the *simplex* type (3 inner salient angles) is virtually absent (0.6% in northern Germany and Denmark; Reichstein & Reise 1965); dental fields of T2, T3 and T4 are occasionally confluent. M_1 is as in *Microtus* s.str.; dental fields of T6, T7 and the anterior cap may be closed. The karyotype (2n=50, NF_a=50) consists of 23 acrocentric and one pair of small metacentric autosomes (Zima & Král 1984). Sex chromosomes contain large blocks of constitutive heterochromatin and are larger than in any other Palaearctic arvicoline; the X and Y chromosomes account for 21.8% and 13.1% of the haploid set, respectively (cf. Zima and Macholán 1995).

Figure 249: Common field vole *Microtus agrestis* from the Czech Republic. Photo courtesy Miloš Anděra.

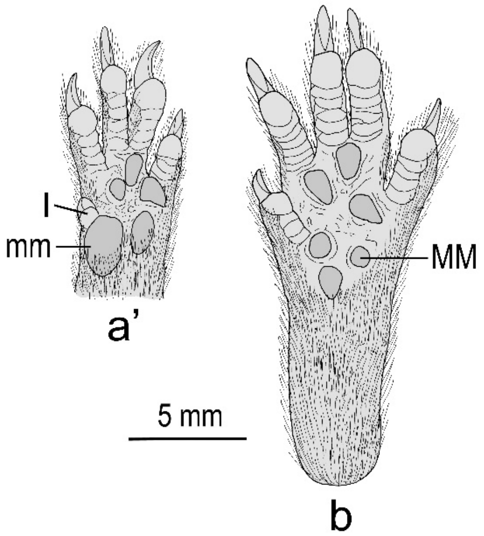


Figure 250: Left palm (a') and sole (b) in *Microtus agrestis* (a'– Norrbotten County, Sweden) and *M. lavernedii* (b– Pohorje Mts., Slovenia).

Key to species

1a) Bullae small (shorter than MxT); Y chromosome 2.7-times longer than the largest autosome; present in Portugal and extreme north-western Spain .... *rozianus*
1b) Bullae larger (longer than MxT); Y chromosome <2-times as long as the largest autosome; present in the rest of Europe and Asia 2
2a) Braincase longer relative to length of skull; present in Southern Europe .... *lavernedii*
2b) Braincase shorter relative to length of skull; present in the rest of Europe and Asia ....*agrestis*

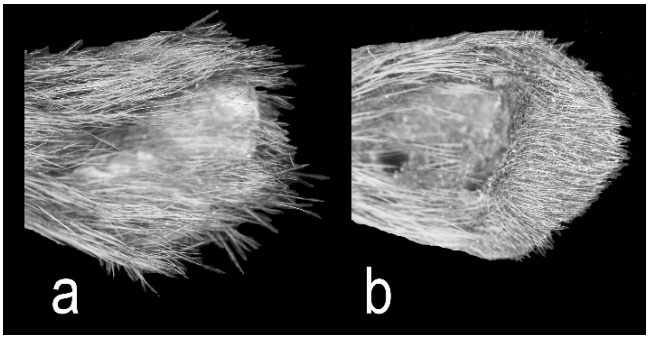


Figure 251: Ear in (a) *Microtus lavernedii* and (b) *M. arvalis* (both from Slovenia). Note the difference in length of hairs. Anterior is to the left and dorsal is at the top. Not to scale.

Microtus agrestis (Linnæus, 1761) – Common Field Vole

Mus agrestis Linnæus, 1761:11. Type locality is "Upsala, Sweden" by subsequent designation (Miller 1912a:668).

Synonyms. *[Mus] gregarius* Linnæus, 1766; *Mus arvalis nigricans* Kerr, 1792 [renaming of *Mus agrestis* Linnaeus]; *Arvicola hirta* Bellamy, 1839; *Arvicola neglecta* Thompson, 1841; *Arv[icola] bailloni* Selys, 1841; *Lemmus insularis* Nilsson, 1844; *A[rvicola] intermedia* Bonaparte, 1845 [nomen nudum]; *A[rvicola] britannicus* Selys, 1847; *[Arvicola agrestis]* Var. *nigra* Fatio, 1869; *Arv[icola] agrestis angustifrons* Fatio, 1905; *[Arvicola agrestis]* var. *nehringi* Rörig & Börner, 1907 [nomen nudum]; *Microtus agrestis exsul* Miller, 1908; *Microtus agrestis mongol* Thomas, 1911; *Microtus arcturus* Thomas, 1912; *Microtus agrestis mial* Barrett-Hamilton & Hinton, 1913; *Microtus agrestis luch* Barrett-Hamilton & Hinton, 1913; *Microtus agrestis macgillivraii* Barrett-Hamilton & Hinton, 1913; *Microtus agrestis fiona* Montagu, 1922; *Microtus agrestis tridentinus* Dal Piaz, 1924; *Microtus agrestis similis* Krausse, 1925 [nomen nudum]; *Microtus agrestis estiae* Reinwaldt, 1927; *Microtus agrestis ognevi* Skalon, 1935; *Microtus agrestis pallida* Melander, 1938; *Microtus agrestis argyropoli* Ognev, 1944; *Microtus agrestis scaloni* Heptner, 1948 [substitute name for *ognevi* Skalon]; *Microtus agrestis argyropuli* Ognev, 1950 [deliberate emendation of *argyropoli* Ognev; not a replacement name for *argyropoli* (Mathias et al. 2017:24)]; *Microtus agrestis armoricanus* Heim de Balsac & de Beaufort, 1966; *Microtus agrestis enez-groezi* Heim de Balsac & de Beaufort, 1966.

Distribution (Figure 254). Widespread from the Atlantic coast of Europe to Lake Baikal and the middle reaches of the Lena River and from the coasts of the North Sea, the Norwegian Sea, the White Sea and the Barents Sea as far south as the Loire and Danube Rivers, to northern Kazakhstan and the Mongolian border. Present in northern France (Alsace, Basse-Normandie, Bourgogne, Bretagne, Centre, Champagne-Ardenne, Franche-Comté, Haute-Normandie, Île-de-France, Lorraine, Nord-Pas-de-Calais, Pays de la Loire, Picardie, Poitou-Charentes), Low Countries, Germany, the majority of Switzerland and Austria (Burgenland, Niederösterreich, Oberösterreich, Salzburg, Steiermark, Tirol, Voralblerg, Wien), marginally present in northern Italy (Trentino-Alto-Adige) and Hungary (Borsod-Abaúj-Zemplén, Gyór-Moson-Sopron, Hajdú-Bihar, Szabolcs-Szatmár-Bereg, Vas), widespread in the Czech Republic, Slovakia, Poland, the Baltic countries, Denmark, throughout Fennoscandia (except for majority of Kola); Romania (the Carpathians, Carpathian Basin and Danube delta), Belarus, northern Ukraine (Cherkassy, Chernigov, Chernivtsi, Ivano-Frankivs'k, Kharkov, Kiev, L'viv, Sumy, Tarnopil', Vinitsa, Zakarpats'ka, Zakarpatskaya, Zhitomir), European Russia (north of Volgograd, Voronezh, Orenburg, Kursk, Bryansk, Tambov, Kaluga, Tula, and Ryazan) and Asian Russian Federation (Chelyabinsk, Sverdlovsk, Khanty-Mansiyskiy Autonomous Okrug, Yamalo-Nenetskiy Autonomous Okrug, Kurgan, Tyumen', Omsk, Novosibirsk, Altai Krai, Altai Republic, Krasnoyarsk, Kemerovo, Khakasiya, Tuva, Irkutsk, Yakutiya). Marginally present in north-eastern

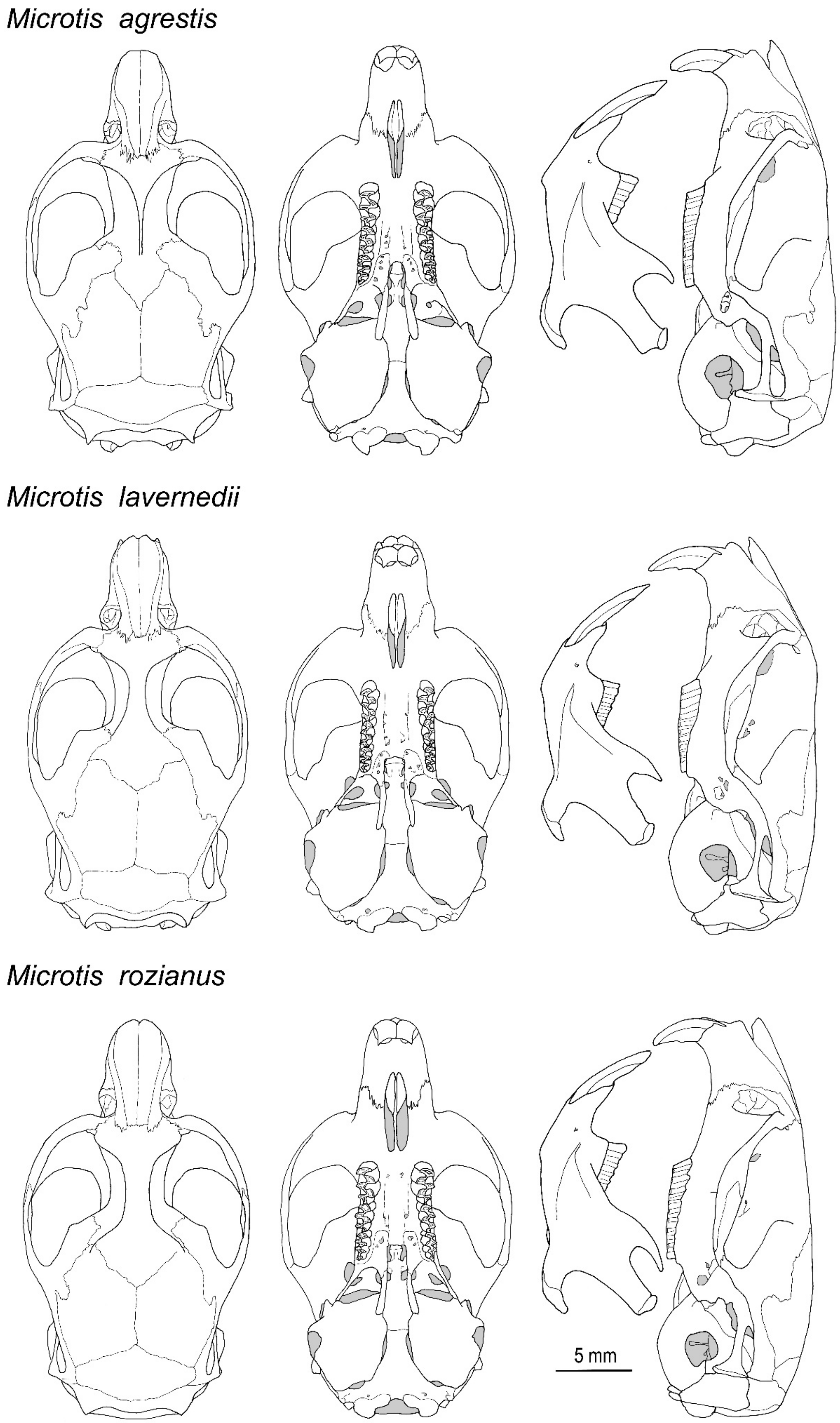


Figure 252: Skull in field voles (top to bottom): top–*Microtus argestis* (near Bergen an der Dumme, Niedersachsen, Germany; top); middle–*M. lavernedii* (near Ljubljana, Slovenia); bottom–*M. rozianus* (15km west of Covilhã, Portugal).

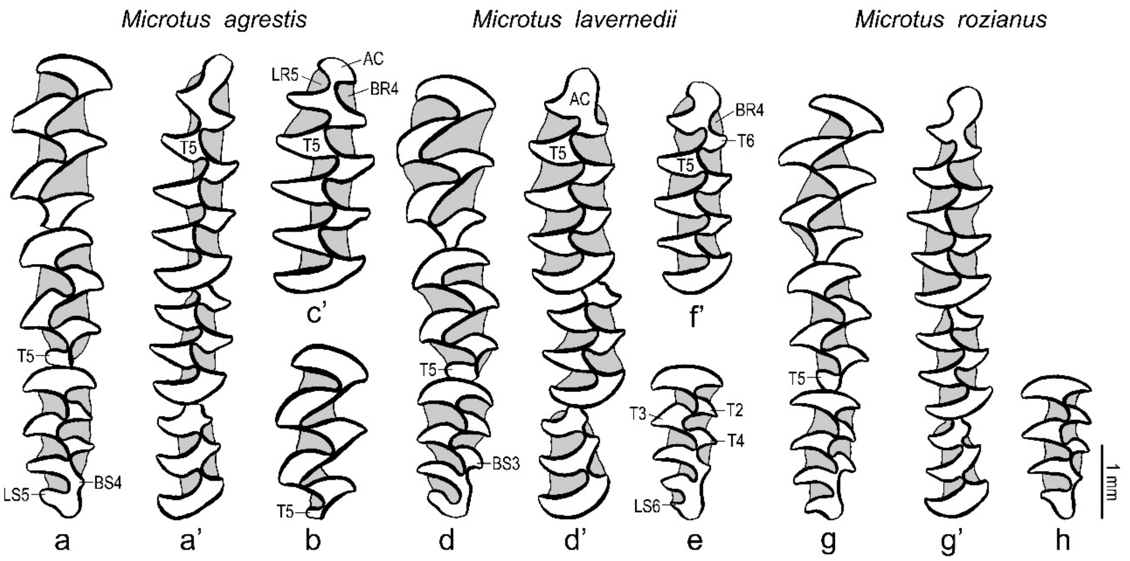


Figure 253: Enamel molar pattern in field voles. *Microtus agrestis*: upper (a) and lower row (a'–Kameničky near Havlíčkův Brod, Czech Republic); isolated M_1 (b–North Uist, Hebrides, Scotland); isolated M^1 (, Smoliany National Park, Mordovia, Russian Federation). *M. lavernedii*: upper (d) and lower row (d'– Picos da Europa, Espinama, Cantabria, Spain); isolated M^3 (e–Turjanci, Slovenia); isolated M_1 (f'–Šentjernej, Slovenia). *M. rozianus*: upper (g) and lower row (g'), and isolated M^3 (h–all from 15km west of Covilhã, Portugal).

Kazakhstan (Shyghys Qazaqstan) and north-western Xinjiang. The range measures 8,185,400 km^2 and the altitudinal range is 0–2,200 m.

Present on a number of European islands where they are only rarely sympatric with *M. arvalis*. Widespread and abundant across Great Britain but absent from Ireland; occupy most of the Outer Hebrides (North Uist, Benbecula, South Uist, Scalpay), Inner Hebrides (Skye, Eigg, Islay, Muck, Mull, Jura, Scarba, Lismore, Gigha, Luing), some other islands offshore western Scotland (Arran, Bute), Wales (Anglesey) and southern England (Wight). Also found offshore the Atlantic coast of France on Groix Island (Bretagne) and Noirmoutie Island (Pays de la Loire), on 2 Frisian (Wadden) Islands offshore the Netherlands (Texel, Ameland), on islands of the North Sea (Sylt offshore Germany; Rømø, Mandø and Fanø off Denmark), on many islands in the Baltic Sea (Ærø, Agersø, Amager, Bågø, Bjørnø, Bornholm, Falster, Fejø, Femø, Fünen, Kidholm, Langeland, Lolland, Lyø, Møn, Nexelø, Store Okseø, Tåsinge, Thurø); Zealand off Denmark, Hiddensee and Rügen off Germany; Abruka, Hanikatsi, Hiiumaa, Saarema and Vormsi offshore Estonia; Åland, Antinmatala, Föglö, Hailuoto, Hermanni, Karlby, Kellon Kraaseli, Kivimo, Kevo, Kökarsören, Kotakari, Rahjan saaristo, Röyttä, Sundskar and a number of small islands near Hanko Peninsula and near Helsinki (Finland); Askö, Gräsö, Hallands Väderö and Öland (Sweden). Also populates the islands along the Kattegat and Skagerrak coasts of Sweden (Orust, Saltö, Rörö, Vargö) and Norway (Austre Seli, Hestholmen, Langøy, Ostøya, Tromøy, Tverrdalsøya), and along the Atlantic coast of Norway (Andørja, Andøya, Austvågøya, Bømlo, Boroyni, Ertvågsøy, Kvaløya, Langøya, Hinnøya, Radøy, Senja, Stokkøya, Stridsholmen, Tjøtta and Vestvågøya) (Niethammer & Krapp 1982, Schlanbusch et al. 2011, Broekhuizen et al. 2016). Local extinctions and recolonisations are frequent in Baltic islands (Ebenhard 1990).

M. agrestis is an unspecialised opportunist living in a variety of habitat types and is virtually independent of the ground water table and type of soil (Myllymäki 1977). Preferred habitats (rough, ungrazed and often damp grassland and young forestry plantations with a lush growth of grass) show rapid secondary succession while low-density habitats are more long-lived (Hansson 1977).

Characteristics. Dimensions: BWt=23–90 g, H&B=104–135 mm, TL=23–51 mm, HF=16–20.2 mm, EL=11–15.5 mm, CbL=23.4–29.7 mm, ZgW=13.1–17.6 mm, MxT=5.8–7.4 mm. Back is tawny-russet to dark brown with the usual admixture of long all-black hairs; sides are paler and washed with buff;

underside is pure grey through which the dusky basal portions of the hairs show here and there. The tail is bicoloured, brown above and like the belly below. Feet are whitish to light ochraceous-buff. Skull is characterised by a comparatively long braincase and large bullae (Figure 252). Molars are as in the subgenus; variation is reported below. The proximal baculum is 2.30–3.00 mm long and 1.30–2.10 mm wide across the basal expansion; on average 1.6–1.8-times longer than wide. Central distal digit measures 0.90–1.20 mm and the tiny lateral digits are slightly longer than half this size (length=0.60–0.80 mm; Aksenova 1980). Karyotype is as in the subgenus. The X chromosome is 2.3–3-times longer and the Y chromosome is 1.5–1.9-times longer than the largest autosome (Fredga & Jaarola 2004).

Variation and subspecies. If *rozianus* and *lavernedii* and their junior synonyms are subtracted from the earlier subspecies lists, the number of recognised subspecific taxa in *agrestis* is 10–15 subspecies, depending on the authority. The difference is due to island races: Ellerman & Morrison-Scott (1951) recognised 5 insular endemics while, like most recent authors, Shenbrot & Krasnov (2005) accepted only *macgillivraii* which is well characterised by a very dark greyish-brown ventral pelage and a complex M^1. Continental races reportedly differ in colour, size and complexity of M^1. Insular populations tend to be larger (Schlanbusch et al. 2011) and have heavier litters which grow faster (Ebenhard 1990). Voles are also larger at high latitude. Proportion of the *exsul* type of M^1 (with T5 present) is typically high (~70–100%) in the north (Great Britain and its islands, Scandinavia, northern European Russia, northern Urals and western Siberia) and <10% at lower latitudes (e.g. Germany, Central and South Russia); the proportion is intermediate (51%) in the Altai and Sayan (Niethammer & Krapp 1982, Cheprakov & Chernousova 2020). In Scotland body size and the presence of *exsul* M^1 increase sharply between the Central Highlands and the north-western Highlands (Lambin 2008) but the character of variation is usually not known in other parts of the range. These traits are known to vary over time. E.g., size reduced over the last 50 years in Estonia but not in Lithuania (Balčiauskienė et al. 2018). For the *exsul* morphotype, Corbet (1975) demonstrated differences in 2 samples from Jura (Inner Hebrides) which were >2,000 years apart; the recent sample displayed a slight reduction in the size of T5. In the Southern Urals, Cheprakov & Chernousova (2020) reported a significant decline in frequency of the *exsul* from 87% to 37% within the same year. Voles from Lyø Island frequently lack T5 on M^2 (Reichstein & Reise 1965).

Field voles from south-western Sweden (south and west of Vänern and Vättern Lakes) are characterised by a peculiar Y chromosome (Lund Y) with much longer

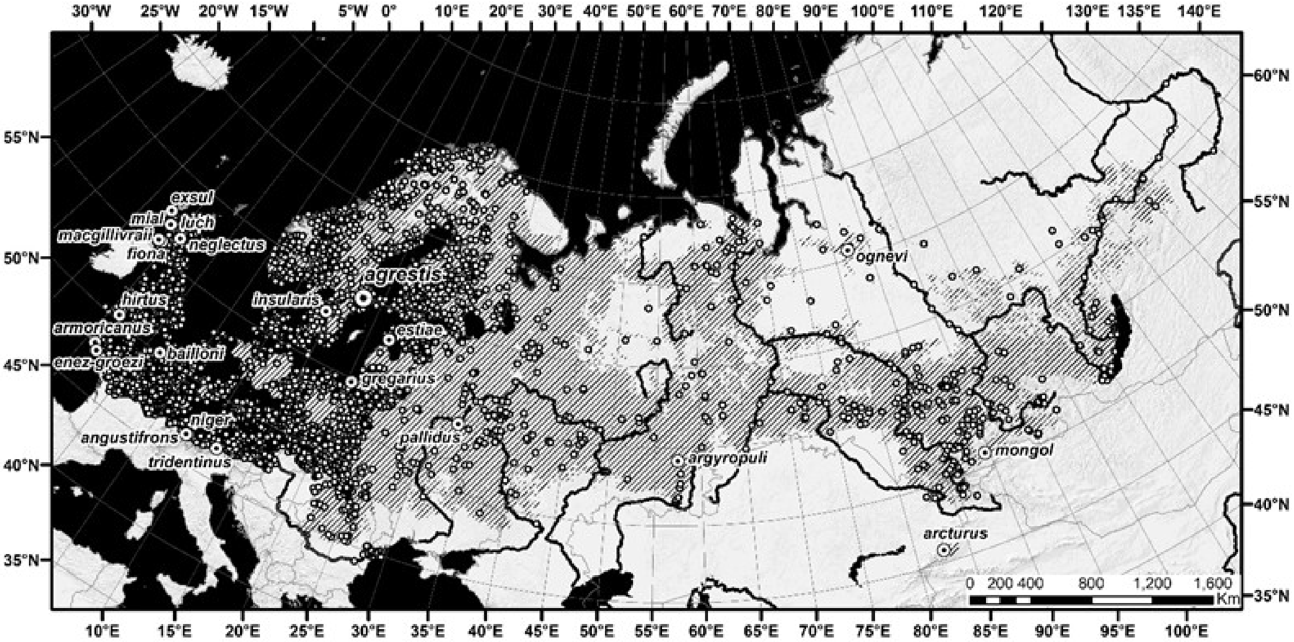


Figure 254: Distributional range of the common field vole *Microtus agrestis*.

euchromatic short arms (barely visible in other populations) which result from pericentric inversion (Fredga & Jaarola 2004).

Phylogeographic screening retrieved two major *Cytb* lineages, the Eastern (Lithuania, eastern Fennoscandia and Russia) and the Western (Jaarola & Searle 2002, Herman & Searle 2011). The latter is further structured into 5 allopatric sublineages: Scandinavian (western Sweden and Norway), Central-European (Belarus, Lithuania, the Czech Republic, Poland, Romania, Denmark), Western-European (the Low Countries, Switzerland, Germany, France, the Czech Republic, southern Great Britain), French (France, Switzerland), and Scottish (northern Great Britain). Current phylogeographic structure was presumably generated by survival in multiple refugia during the Last Glacial Maximum and the subsequent expansion of populations that went through bottlenecks during the Younger Dryas (~12 kya) (Herman & Searle 2011).

Microtus lavernedii (Crespon, 1844) – Mediterranean Field Vole

A[rvicola] lavernedii Crespon, 1844:73. Type locality: "between St. Gilles and Aiguesmortes [Aigues-Mortes]", Gard department, Occitanie region, southern France.

Synonyms. *[Arvicola agrestis]* [forme] *rufa* Fatio, 1900; *Arv[icola] agrestis, latifrons* Fatio, 1905; *Microtus agrestis punctus* Montagu, 1923; *Microtus agrestis pannonicus* Éhik, 1924; *Microtus agrestis Wettsteini* Éhik, 1928; *Microtus agrestis carinthiacus* Kretzoi, 1958 [replacement name for *wettsteini* Éhik].

Taxonomy and nomenclature. *M. lavernedii* is eponym of E. Thomas de Lavernède, therefore *levernedii* is the incorrect subsequent spelling (cf. Wettstein-Westerheimb 1959:683) which was unintentionally introduced by Miller (1912a:671). Because of the enormous influence of Miller's work and since his *lapsus* has been repeated in the mainstream taxonomic literature, the incorrect spelling is now in general use.

The Mediterranean field vole was never recognised as a species in its own right in the past, usually being classified as a subspecies of *agrestis* or even a synonym of *bailloni* (e.g. Niethammer 1964, Castells & Mayo 1993). Several of its junior synonyms were occasionally treated as independent subspecies of *agrestis* but were never formally merged with *lavernedii*. Current status is based entirely on molecular evidence. *M. lavernedii* is closely related to *agrestis* and some estimates suggest TMRCA <20 kya (Paupério et al. 2012). Localised hybridisation with limited gene flow was found in the contact zone in the Swiss Jura (Beysard et al. 2012).

Distribution (Figure 255). Endemic to western Mediterranean Europe in northern Spain (Aragon, Asturias, Alava, Barcelona, Burgos, Cantabria, Castilla y León, Cataluña, Galicia, Gipuzkoa, Girona, Huesca, La Rioja, León, Lleida, Navarra, País Vasco, Vizcaya, Palencia, Soria, Valladolid, Zamora, Zaragoza), Andorra, South France (Alpes-Côte d'Azur, Aquitaine, Auvergne, Bourgogne, Centre, Franche-Comté, Languedoc-Roussillon, Limousin, Midi-Pyrénées, Pays de la Loire, Poitou-Charentes, Rhône-Alpes), south-western Switzerland (Bern, Freiburg, Genève, Graubünden, Neuchâtel, Vaud, Wallis), north-eastern Italy (Friuli-Venezia Giulia, Lombardia, Trentino-Alto Adige, Veneto), southern Austria (Kärnten and Steiermark, marginally in Burgenland, Tirol and Salzburg), Slovenia (except the south-western part), western Hungary (Bács-Kiskun, Baranya, Csongrád, Fejér, Gyór-Moson-Sopron, Nógrád, Pest, Somogy, Tolna, Vas, Veszprém, Zala), northern Croatia, very marginally in northern Bosnia and Herzegovina and north-western Serbia (Voivodina). The range is in two fragments, the western (Switzerland and westward) and the eastern (Italy and eastward). Distributional area covers an estimated 516,790 km^2 and the altitudinal range is from sea level to 2,600 m. Habitat preferences are similar to *agrestis*; in the Mediterranean climate the species can be found on sites with a high ground water table and lush grasses and herbs.

Characteristics. Dimensions: BWt=20.5–59 g, H&B=97–140 mm, TL=26–51 mm, HF=14.7–21 mm, EL=10–15.1 mm, CbL=25.2–28.9 mm, ZgW=13.9–16.6 mm, MxT=6.0–7.4 mm. *M. lavernedii* does not differ from *agrestis* except that the braincase is on average relatively longer. The only baculum figured in Anderson (1960; as *agrestis*) is the same size as *agrestis* (length of the

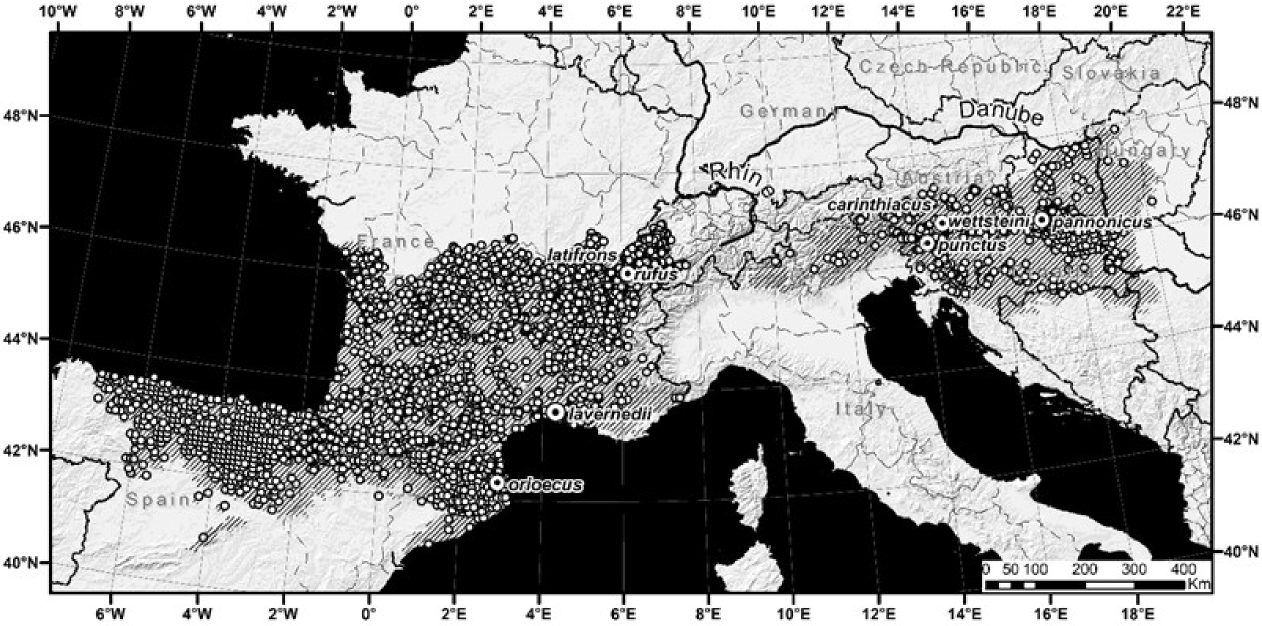


Figure 255: Distributional range of the Mediterranean field vole *Microtus lavernedii*.

proximal baculum=2.9 mm), but has a narrower base and is therefore 1.9-times longer than wide. The lateral digits are smaller and the stalk is dorso-ventrally deeper than in *agrestis*. Karyotype is as in the subgenus (Král et al. 1979; J. Zima personal communication).

Variation and subspecies. Subspecific taxonomy is not settled. Niethammer & Krapp (1982) synonymised the majority of junior synonyms of *lavernedii* (*punctus, pannonicus* and *carinthiacus*) with *nigra* (a junior synonym of *agrestis*); in the same source, *orioecus* is a junior synonym of *gregarius* and *lavernedii* is listed as an independent subspecies. On the other hand, Ellerman & Morrison-Scott (1951) and Shenbrot & Krasnov (2005) listed 4 names, all junior synonyms of *lavernedii*, as independent subspecies.

Microtus rozianus (Bocage, 1865) – Portugese Field Vole

Arvicola Rozianus Bocage, 1865:7. Type locality: "Habitat apud Conimbricam" i.e. "near Coimbra, in [county of] Geria", Portugal.

Nomenclature. Issues of the *Memorias da Academia Real das Sciencias de Lisboa* were released separately, each with pagination starting anew and the year of release is not evident on the front cover. Volume 3(2) with Bocage's paper has the year 1865 on the title page, which is also quoted by Miller (1912a:680), Almaça (1993) and Mathias et al. (2017:24); Lataste (1883b:373) and Cabrera (1914:282) quoted 1864 as the year of publication.

Taxonomy. Status of *rozianus* as an independent species rests on multilocus phylogenetic reconstructions which retrieved a sister position of *rozianus* against *agrestis*+*lavernedii*; TMRCA was estimated at ~70 kya. There is no unambiguous indication of genetic exchange between *rozianus* and *lavernedii* (Paupério et al. 2012). In the past *rozianus* was regarded as a synonym of *agrestis* (e.g. Trouessart 1897), its subspecies (Miller 1912a), or was synonymised with *bailloni* (Niethammer 1970b) or *gregarius* (Niethammer & Krapp 1982).

Distribution (Figure 256). Endemic to the north-western Iberian Peninsula in Portugal (Aveiro, Braga, Bragança, Castelo Branco, Coimbra, Guarda, Leiria, Santarem, Viana do Castelo, Vila Real, Viseu) and adjacent Castilla y León, Extremadura and Galicia in Spain. Occurs at low abundance in humid grassy habitats including coastal marshland and reed beds; elevational range is from sea level up to 1,775 m. The range of 76,685 km² is thought to be shrinking as a result of the current rate of climate change (Fletcher et al. 2019).

Characteristics. Size, although rather small, is well within the range for *agrestis* or *lavernedii*: BWt=38–39 g, H&B=104–106 mm, TL=38–41 mm, HF=18–19 mm, EL=12 mm, CbL=22.9–27.7 mm, ZgW=13.2–16.5 mm, MxT=5.6–7.3 mm. Tail is sparsely covered by hair and the annulation is largely exposed. Dorsal fur is clear brown with yellow or rusty wash; flanks are more clear yellowish and are demarcated from a pure grey underside. Feet are light-grey and the ears are brown-grey; tail is indistinctly bi-chromatic, dark brown above and grey below. The skull differs chiefly in smaller bullae (Figure 252) which are shorter than the maxillary tooth-row (longer than MxT in *agrestis* and *lavernedii*). The dorsal profile is evenly bowed and the zygomatic arches are fairly expanded (ZgW/CbL=0.58). Molars show no peculiarities (Figure 253g,h). The postero-lingual triangle T5 is well-developed in ~35% of M^1 specimens and absent in another ~35%. M^3 has 3 or 4 inner salient angles in a balanced 1:1 ratio (Almaça 1993). Karyotype is as in *agrestis*; the Y chromosome is comparatively larger (2.7-times longer than the largest autosome) and has slightly longer short arms (Giménez et al. 2012).

Variation and subspecies. Monotypic.

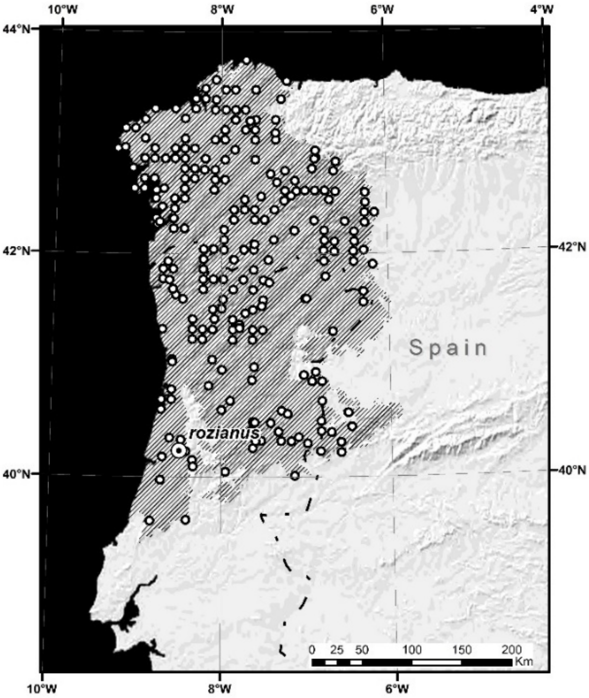


Figure 256: Distributional range of the Portugese field vole *Microtus rozianus*.

SUBGENUS: *Iberomys* Chaline, 1972 – Cabrera's Voles

Iberomys Chaline 1972:120. Type species is *Microtus dentatus* Miller (=*Microtus cabrerae*).

Microtus cabrerae Thomas, 1906 – Cabrera's Vole

Microtus Cabrerae Thomas, 1906c:576. Type locality: "Sierra de Guadarrama, near Rascafria, N[orth] of Madrid. Altitude about 1000–1300 m" (p. 577), Spain.

Synonyms. *Microtus dentatus* Miller, 1910; *Microtus cabrerai* Trouessart, 1910 [unjustified emmendation of *cabrerae* Thomas].

Taxonomy. Cabrera's vole was traditionally regarded as a close relative of *M. arvalis* and classified as a subgenus *Microtus*. In the 1970s, Chaline (1972) proposed *Iberomys* (as a subgenus of *Microtus*) for the current *dentatus* (the type species) and *cabrerae*, along with several fossil taxa. Shortly afterwards, Chaline (1974) transferred *cabrerae* to *Arvalomys* (type species is *Microtus arvalis*) while leaving *dentatus* in *Iberomys*. *Iberomys* was resurrected in DNA-based phylogenetic reconstructions (Jaarola et al. 2004) and some Iberian authors started to use it as a genus in its own right, firstly in palaeontology (e.g. Cuenca Bescós et al. 2014) and afterwards in zoology (Garrido-García et al. 2013).

Classification of *cabrerae* into a monospecific (sub)genus, however, does not resolve its phylogenetic relationships in *Microtus*. Recent reconstructions either left the position of *cabrerae* unresolved (e.g. Fink et al. 2010) or classified it with the Nearctic *Microtus* (Robovský et al. 2008, Martínková & Moravec 2012). Barbosa et al. (2018) proposed sister relationships between *cabrerae* and *agrestis* s.lat., and classified both in the subgenus *Agricola*. Both *agrestis* and *cabrerae* have giant sex chromosomes with large blocks of constitutive heterochromatin which evolved independently (Fernández et al. 2001). Argyropulo (1933) suggested that *cabrerae* might connect

Summeriomys (here a species group *socialis* in the subgenus *Microtus*) and *Microtus* proper, which was followed by some authors. Ellerman (1941) classified *cabrerae* into his species group *guentheri* and Brink (1956) even synonymised the two species. Cuenca Bescós et al. (2014) put forward putative phylogenetic links between *Iberomys* and *Stenocranius*. The fossil record of *Iberomys* can be traced back to the end of the Early Pleistocene and the extant species putatively appeared during the late Middle Pleistocene (Laplana & Sevilla 2013).

Distribution (Figure 257). Endemic to the Iberian Peninsula and present in Spain (Andalucía, Aragón, Castilla y León, Castilla-La Mancha, Extremadura, Madrid, Murcia, Navarra, Valencia) and Portugal (Beja, Bragança, Castelo Branco, Évora, Faro, Guarda, Leiria, Portalegre, Santarém, Setúbal). The range (area=141,740 km^2) is fragmented at various spatial scales. On the large scale, 4 major fragments are obvious, the western (Luso-Carpetanian sensu Garrido-García et al. 2013), the northern (Prepyrenean), the southern (Baetic) and the eastern (Montiberian). At the landscape scale, the colonies are small (mean diameter≈50 m) and far apart with the average distance of the nearest neighbour at ~365 m. Historical range was more extensive also encompassing northern and southern Spain, and until the Middle Ages, the coastal areas of the Balearic Sea and the Gulf of Lyon in southern France (Laplana & Sevilla 2013). Range contraction was ascribed to climate change (Laplana & Sevilla 2013) or intensification in agriculture (Garrido-García et al. 2017). *M. cabrerae* occupy discrete tall herb patches scattered across the agricultural landscape (Pita et al. 2014) which are associated with a high water table or are periodically flooded. Altitudinal range is from sea level up to 1,975 m and medium elevations are preferred.

Characteristics. Dimensions: BWt=30–78 g, H&B=100–135 mm, TL=30–52 mm, HF=18.2–22 mm, EL=9.8–16.6 mm, CbL=25.0–30.6 mm, ZgW=14.7–18.8 mm, MxT=5.6–7.4 mm (Ventura et

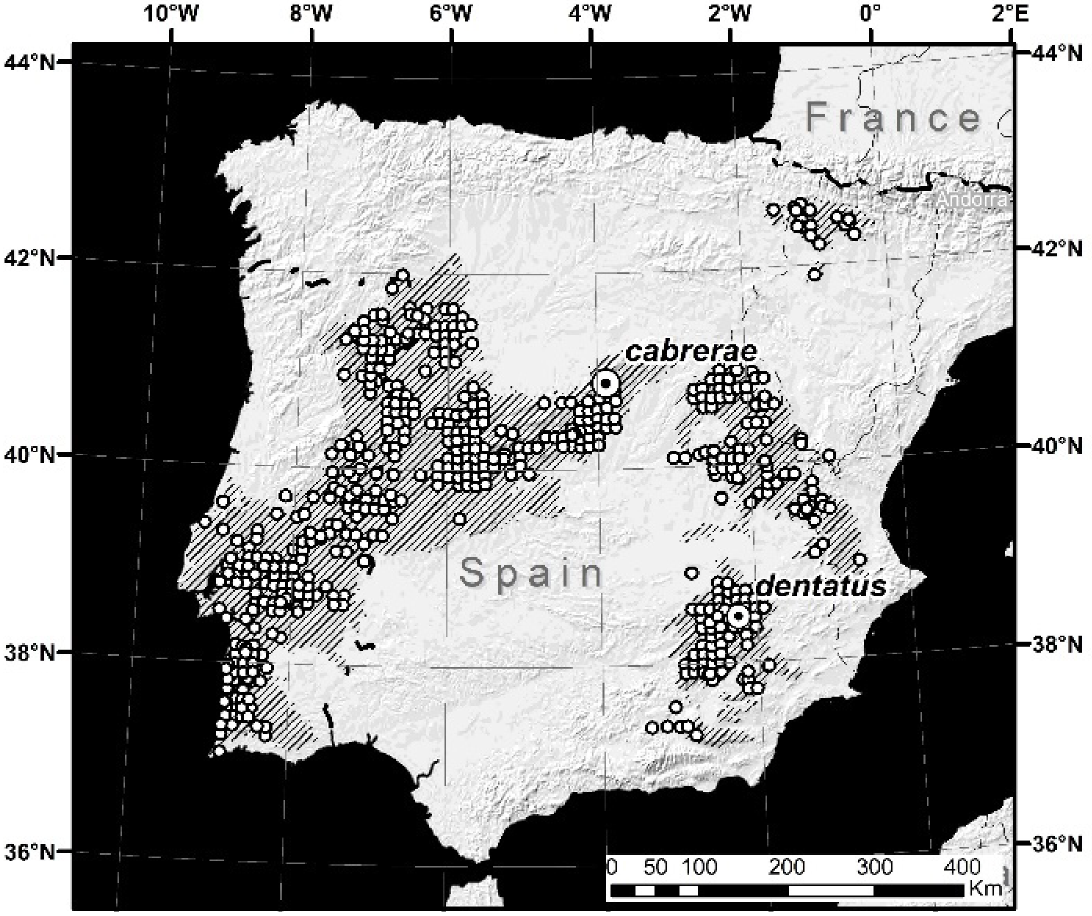


Figure 257: Distributional range of Cabrera's vole *Microtus cabrerae*.

al. 1998). Form and appearance (Figure 258) are typical for the subgenus *Microtus*. The tail is of comparable relative length (TL/H&B=0.31–0.37) and the ears are almost completely clad with hair; there are 6 plantar pads and females have 8 nipples. Vibrissae are on average longer, the fur is thicker and the protruding hairs on the back and rump are conspicuously long (17–19 mm). Upper parts are yellowish brown with variable effect of grizzling due to pale tips or sub-terminal annulations of protruding hairs; the effect is strengthened by the presence of long all-black hairs. The flanks are clear ochraceous-buff and the underparts are silvery grey to dull grey, always clouded by the slate-grey hair bases and commonly suffused with cream or buff shades; there is no evident line of demarcation along the sides. The tail is usually inconspicuously bi-chromatic, brownish or blackish above and whitish below; feet are dull-whitish. The baculum is of trident type but the distal portion is reduced (Niethammer et al. 1964); the proximal bone is 3.2 mm long and 1.5 mm wide across the basal expansion; of the distal baculum, the central digit is roundish (0.8 mm long and 0.65 mm wide) and lateral digits are particularly small (length=0.4 mm).

Figure 258: Cabrera's voles *Microtus cabrerae* from Jaén Province, Spain. Photo José A. Garrido García.

Skull, although of average proportions (ZgW/CbL=0.58–0.60), differs in many respects (Figure 259). The dorsal profile is evenly bowed and the braincase is deep (height behind M^3≈40% CbL). The nasal bones are of approximately the same length as the diastema or longer (in *Microtus* proper, the nasals are normally shorter than the diastema); incisive foramens are wide and the postorbital processes of the squamous bone are marked. Adult skull does not develop the interorbital crest but subadult crania show evident longitudinal furrow in the orbital region. The root of the lower incisor terminates immediately behind M_3 and therefore shows only a rudimentary upward extension. For this reason, the broad bony swelling on the lingual side of the ascending ramus, which is typical of *Microtus* and allied genera, is absent in Cabrera's vole. Instead, there is a narrow bony crest with the mandibular foramen at the very margin of the

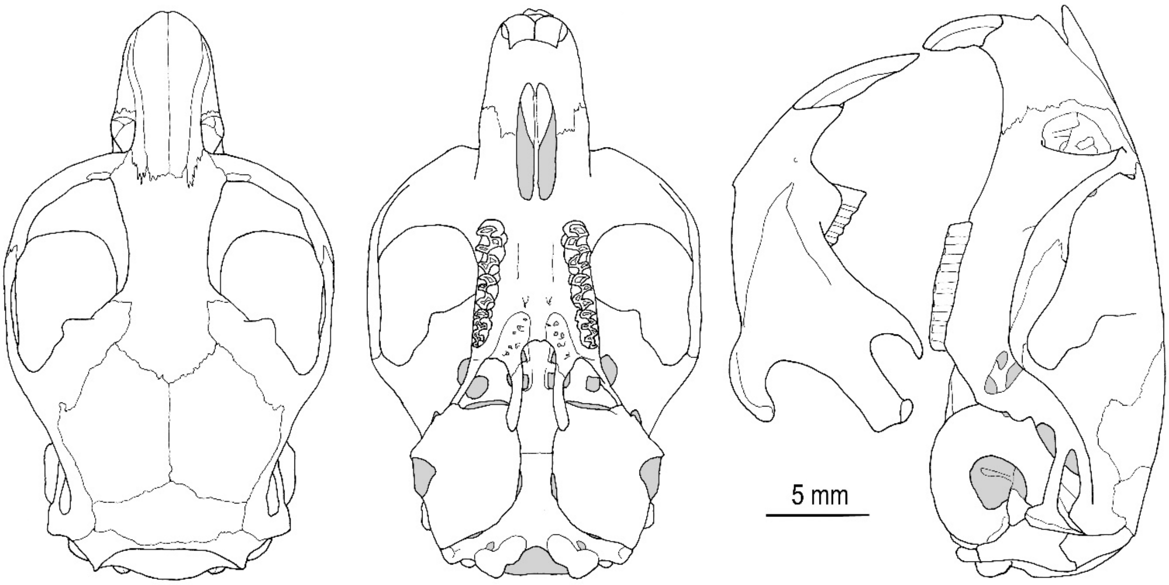


Figure 259: Skull in *Microtus cabrerae* from Sa. de Cazorla, Spain.

posterior *incisura mandibulae*; furthermore, the pterygoid fossa is more extensive (Figure 260).

The molars are wide relative to length and the terminal lobe of M_1 is short. Triangles are frequently compressed in the anterior-posterior direction which allows for the expansion of re-entrant angles. The labial triangles are decidedly smaller than the lingual ones. M^1 and M^2 usually show a constricted base and outward turning of the enamel bands; the anterior part of M_2 can be of similar shape. M^3 often has 3 inner and 3 outer re-entrant angles; an additional re-entrant fold (LR4) is rare and the posterior cap is occasionally isolated from dental field T5. M_1: dental field of T5 is always closed and the antero-labial salient angle BS4 is of variable shape but never closed; the labial re-entrant angle BR4 is rarely present as a shallow anticline. The antero-lingual re-entrant angle LR4 is deep (Figure 261); the AC is of a deltoid outline although its size and shape vary a great deal (cf. Fig. 3 in López-García et al. 2020). M_3: dental fields T1 and T2 are separated in 29–61% of voles, depending on the population (Ventura et al. 1998).

Karyotype: 2n=54, NF_a=60; 4 autosomal pairs are bi-armed and heterosomes are gigantic; the X chromosome is submetacentric and the largest in the set; the Y is subtelocentric and the same size as the

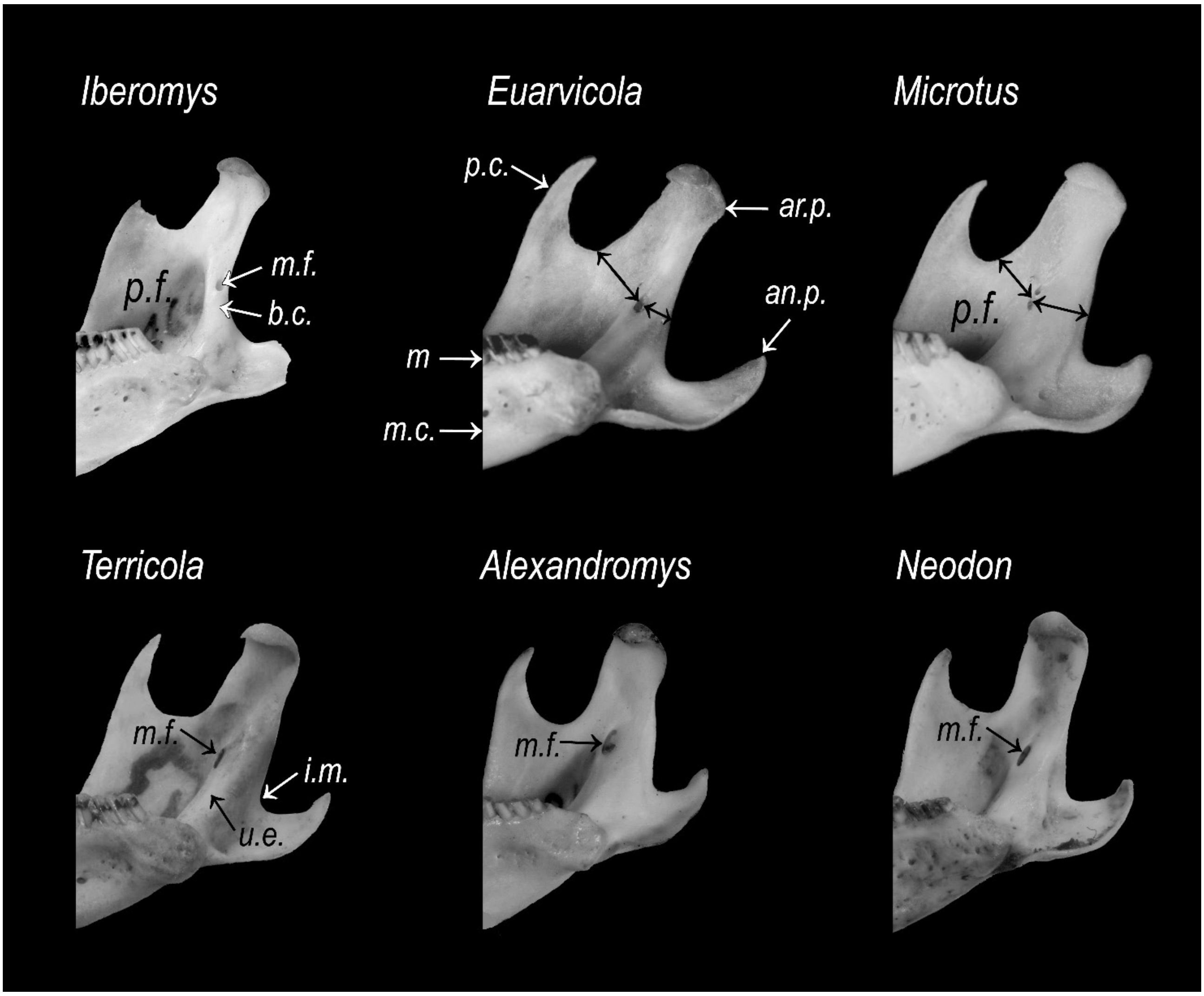


Figure 260: Lingual side of right mandibular ramus in *Microtus (Iberomys) cabrerae* and related voles (left-to-right, upper row: *M. (Euarvicola) lavernedii; M. (Microtus) rossiaemeridionalis*. Bottom row: *M. (Terricola) savii; Alexandromys montebelli, Neodon sikimensis*. Not to scale. Left-right arrows show the distance of the mandibular foramen from the anterior and the posterior margin of mandibular ramus, respectively. Abbreviations: *an.p.* –angular process; *ar.p.* –articular process; *b.c.*–bony crest; *i.m.*–posterior *incisura mandibulae*; *m*–molar row; *m.c.* –mandibular body; *m.f.*–mandibular foramen; *p.c.* –coronoid process; *p.f.*–pterygoid fossa; *u.e.*–upward extension of incisor root.

largest autosome (Zima & Král 1984). Both sex chromosomes are characterised by large segments of constitutive heterochromatin. The *Sry*-gene is not male-specific and is present in multiple, polymorphic copies in both males and females; this gene is male-specific in *Euarvicola* (Bullejos et al. 1997).

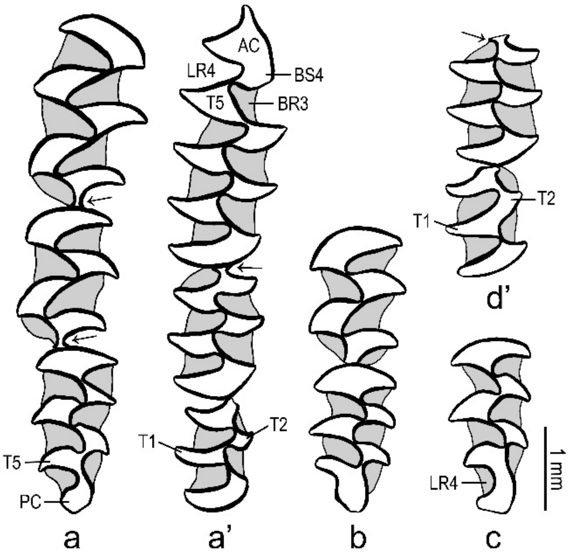


Figure 261: Occlusial molar pattern in *Microtus cabrerae*: upper (a) and lower row (a'); isolated $M^{2–3}$ (b), M^3 (c), and $M_{2–3}$ (d'). Arrows point to the narrow molar base on $M^{1–2}$ and M_2; note the outward turning of the enamel bands. Vouchers are from Sa. de Cazorla (a–c) and Sierra de Guadarrama (d'), Spain.

Variation and subspecies. Monotypic (Ventura et al. 1998).

SUBGENUS: *Terricola* Fatio, 1867 – Pine voles

Terricola Fatio, 1867:73 (footnote). Type species by subsequent designation (Lataste 1883q:349) is *Arvicola subterraneus* Sélys.

Synonyms. *Micrurus* Major, 1877 [preoccupied by Ehrenberg 1831 for Nemertea]; *Arbusticola* Shidlovskiy, 1919; *Meridiopitymys* Chaline, 1974; *Parapitymys* Chaline & Mein. 1979.

Nomenclature. *Terricola* Fatio is preoccupied by *Terricola* Fleming (1828:225) which was introduced as one of the two series of the gastropod molluscan subgroup Pulmonifera with no formal ranking; not used in Fleming (1842) or in later indexes of zoological nomenclature (Kryštufek et al. 1996). *Terricola* Fleming is therefore not available for nomenclatural purposes.

Taxonomy. The subgenus *Terricola* contains voles with confluent dental fields T4–T5 on M^1 (the so-called "pitymyan rhombus"; Brunet-Lecomte & Chaline 1991) which occupy the south-western Palaearctic. In the past these voles were classified in *Pitymys* McMurtrie, 1841 (the Nearctic *Psammomy pinetorum* Conte, 1830 is the type species). Mammalogists ranked *Pitymys* either as a genus in its own right, or, more frequently, as a subgenus of *Microtus*. Defined in this manner, *Pitymys* contained Nearctic pine voles and Palaearctic taxa which are now classified in *Neodon* and several groups of *Microtus*. Of these species, *schelkovnikovi* was retained in *Terricola* until recently.

Schulze (1900:204) previously used *Terricola* as a subgenus of *Hypudaeus* for *subterraneus* and *savii*. Russian authors infrequently used other genus-group names such as *Arbusticola* (Ognev 1924) or *Micrurus* (Kuzyakin 1963). Currently, *Terricola* is ranked as a subgenus of *Microtus* (Brunet-Lecomte & Chaline 1991, Zagorodnyuk 1993, Gromov & Erbajeva 1995, Rekovec 1994, Pavlinov et al. 1995, Pavlinov & Rossolimo 1998, Chaline et al. 1999, Kowalski 2001, Robovský et al. 2008, Pardiñas et al. 2017). The opinion that *Terricola* deserves full generic ranking is common in palaeontology but is rare among neozoologists (Zagorodnyuk 1990, Baskevich 1997, Romanenko et al. 2018).

With the exception of Ellerman & Morrison-Scott (1951), who recognised only 3 species of pine voles, the majority of taxonomists acknowledged higher species richness, e.g. 17 species in Trouessart (1910) and 19 species in Miller (1912a) for Europe alone. Species delimitation has always been a thorny issue in this group and early authors (Sélys 1839, Gerbe 1854, Minà-Palumbo 1868) introduced unconventional auxillary traits such as the number of vertebrae. Species delimitation started progressing with the introduction of chromosomal analyses in the 1950s (Matthey 1954, 1955).

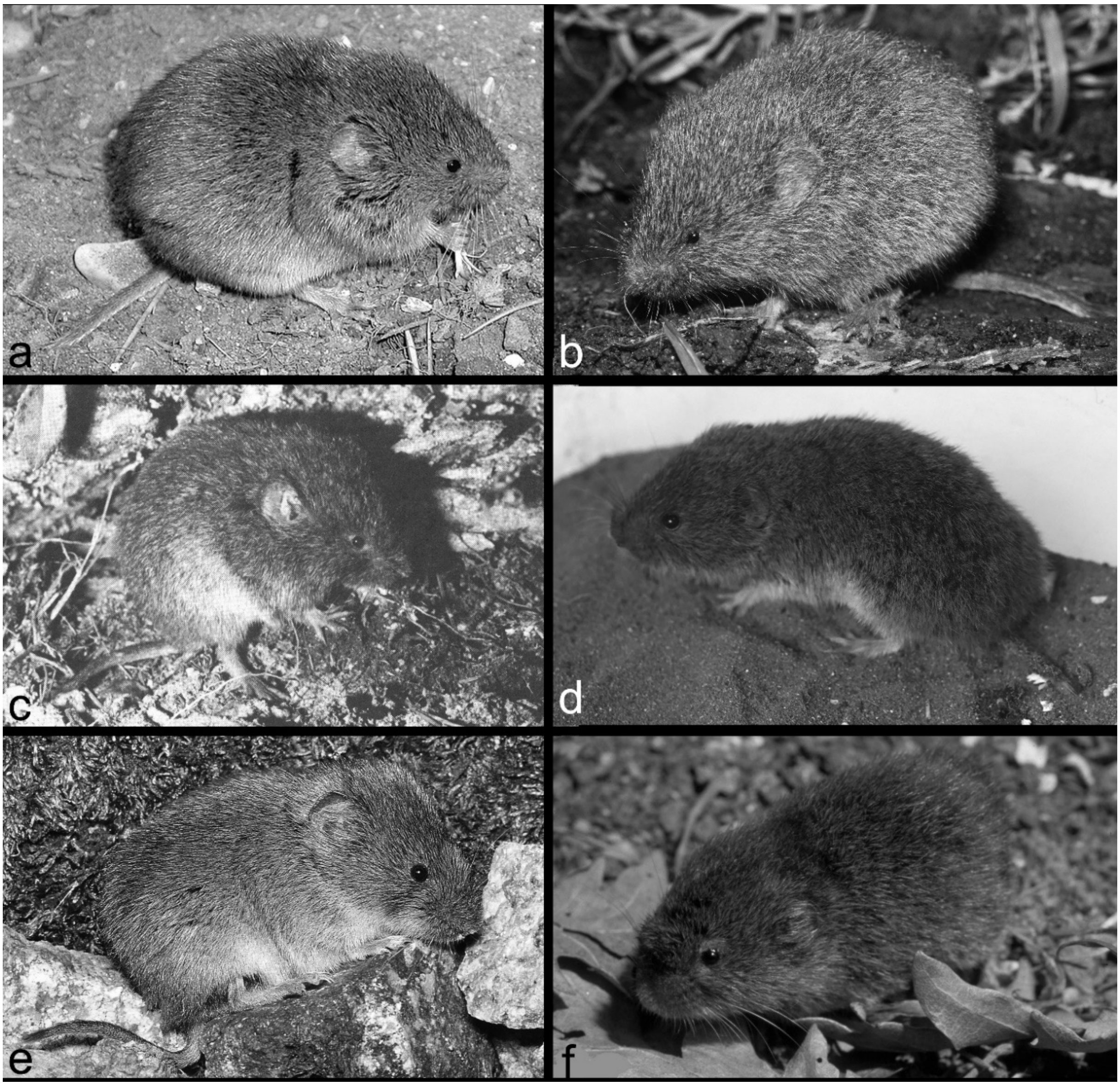


Figure 262: Representatives of pine voles: a,b–*Microtus subterraneus* from Cığlıkara, Antalya, Turkey (a) and the Czech Republic (b); c–*M. liechtensteini* (Mt. Snežnik, Slovenia); d–*M. thomasi* (northern Peloponnese, Greece); e–*M. tatricus* (Slovakia); f–*M savii* (vicinity of Rome, Italy). Photo by Alenka Kryštufek (a), Miloš Anděra (b), Jaroslav Červený (c), Boris Kryštufek (d), Pavel Rödl (e), Dario Capizzi (f).

There is little consensus regarding the grouping of pine vole species. Chaline et al. (1999) proposed a basal dichotomy of *Terricola* into two lineages, the Mediterranean (*duodecimcostatus, lusitanicus*, and *savii*) and the Middle-European (remaining species); Zagorodnyuk (1990) ranked these groups as subgenera, *Meridiopitymys* (*savii, gerbei, duodecimcostatus, thomasi*) and *Terricola* s.str.; Miller (1912a) recognised 3 groups, the *subterraneus,* the *savii,* and the *ibericus* (=*duodecimcostatus*), based on the complexity of M^3, and Russian authors (Pavlinov & Rossolimo 1987) added the *majori* group to this number (with *majori* and *schelkovnikovi*). Kratochvíl & Král (1974) distinguished 5 groups: (i) Gallo-Iberian (*duodecimcostatus, lusitanicus, gerbei=pyraneicus*), (2) Central European-Apennine (*subterraneus* and *savii* groups), (3) Alpine (*multiplex* and *liechtensteini*), (4) the Aegean (*thomasi*), and (5) the Carpathian (*tatricus*). We classify pine voles into 5 species groups which show strong geographic associations. The basal groups (*majori* and *subterraneus* species groups) are both present in the eastern part of the current range in south-western Asia.

The appearance of *Terricola* in the fossil record is variously given as the Middle Pleistocene (Kurtén 1968), Lower Pleistocene (Kowalski 2001) or Upper

Pliocene (Pavlinov et al. 1995). Brunet-Lecomte (1990) claimed that the basal divergence occurred 700 kya and Tougard (2017) estimated that the subgenus emerged in the Early Pliocene 4.05 Mya. Meylan (1974) concluded from interspecific hybridisation trials and chromosomal data that speciation in *Terricola* had to be a comparatively recent phenomenon. Interspecific crossbreeding trials yielded offspring in the majority of cases, however hybrid males were normally sterile.

Distribution. Range extends from the Atlantic coast as far east as the Volga River and the Caspian Sea, and from the Baltic coast and Lake Onega to the Mediterranean coast. The majority of species occupy traditional Mediterranean refugia. Pine voles are absent from the islands with the exception of Sicily and Euboea (Greece). They are more fossorial on average than other *Microtus* voles and prefer soft and humid soil.

Characteristics. Small and short-tailed voles with tiny eyes (Figure 262); short and soft fur is of mole-like texture. Ears are concealed in the hair. Hind foot has 5 (rarely 6) pads; interdigital pads are of approximately the same size as the medial metatarsal pad or even larger (Figure 263). Claws are slightly lengthened and of approximately the same length in the front and hind feet. Nipples are reduced to 2 inguinal pairs and an additional pectoral pair is retained in only a few taxa; rump glands are present in males. Skull is lightly built and modified for fossorial life. Braincase is smooth and depressed, temporal ridges are weakly developed and remain widely apart. Palate is as in *Microtus*, palatal fossae are deep, bullae are swollen and the incisive foramina are comparatively short. Mandible shows no peculiarities; the alveolar process is prominent in strictly fossorial species which also normally display proodont upper incisors (Figure 264). Molar pattern is similar to *Microtus* except for a pitymoyd M_1, i.e. the triangles T4–T5 are confluent. Cement is present in the re-entrant angles. The baculum is of the typical arvicoline trident structure (Figure 265). Diploid number of chromosomes varies between 32 and 62 (NF_a=38–78); the majority of species have 2n=54 and NF_a=56 or 58. Karyotype is frequently polymorphic and the diploid number is variable in 3 species. At least some *Terricola* voles shifted towards the K-end of the r-K continuum of the *Microtus* scale (Guédon et al. 1991).

Key to species

1a) M^3 with 3 lingual salient angles, normally longer than M^2 ……………….. 2

1b) M^3 with 2 lingual salient angles, normally shorter than M^2 ……………….. 8

2a) Females with 6 nipples; present in the Caucasus and south-western Asia east of ~37th meridian ………………………………………………………… 3

2b) Females with 4 nipples; present in Europe and south-western Asia west of ~40th meridian ………………………………………………………… 4

3a) Interorbital constriction ≤3.9 mm; height of skull across molars <7.6 mm; orbital region concave in profile view. M_1: triangles tend to be squeezed; re-entrant angles BR4 and LR5 frequently deep, restricting connection between the anterior cap and triangles T6–7; length of sperm head ≥6.7 µm ………………………………………… *daghestanicus*

3b) Interorbital constriction ≥3.9 mm; height of skull across molars >7.6 mm; dorsal profile straight or slightly convex. M_1: triangles tend to be wide; re-entrant angles BR4 and LR5 frequently shallow, leaving a wide connection between the anterior cap and triangles T6–7; length of sperm head ≤6.7 µm ………………………………………….… *majori*

4a) 6 plantar pads ………................................ *tatricus*

4b) 5 plantar pads ………………......................... 5

5a) Ears longer, usually >7.5 mm; skull shallower with a flat dorsal profile behind the nasals; 2n>50 …………………………………………….............. 6

5b) Ears shorter, usually <8 mm; skull deeper with convex dorsal profile; 2n<50 ……………………...... 7

6a) Present in the Black Sea region of Turkey ……………………….................................. *fingeri*

6b) Present in Europe and the Aegean coast of Turkey …………….. *subterraneus*

7a) 2n=48; present west of ~11th meridian ……………………………...................... *multiplex*

7b) 2n=46; present east of ~11th meridian ……………………….......................... *liechtensteini*

8a) Present west of the 4th meridian …………….... 9

8b) Present east of the 6th meridian ……………... 11

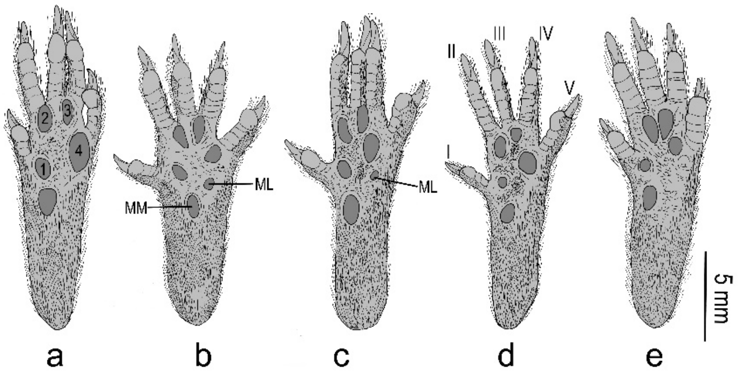


Figure 263: Plantar surfaces in pine voles (subgenus *Terricola*): a–*M. majori* (Meryemana, Trabzon, Turkey), b– *M. savii* (Cascinelle, Lombardia, Italy), c–*M. tatricus* (Vel'ká Fatra Mts., Slovakia), d–*M. felteni* (Karadjica, North Macedonia), and e–*M. thomasi* (northern Peloponnes, Greece). Digits are shown in Roman numerals (thumb = I) and interdigital pads are shown in Arabic numbers. Metatarsal pads are specified by lower and upper case letters, respectively: mm/MM–medial pad, ml/ML–lateral pad.

9a) T2 larger on M^3, its dental field frequently isolated; nasals narrower, their width <42% of the nasal length; 2n=54 …………………………................… *pyrenaicus*

9b) T2 smaller on M^3, its dental field communicates with T3; nasals broader, their width >41% of the nasal length; 2n=62 ……………………….……………….…….. 10

10a) Larger; length of diastem >7.5 mm; upper incisors distinctly proodont; alveolar process on the lingual wall of the mandibular ramus is prominent ……………………………………… *duodecimcostatus*

10b) Smaller; length of diastem <7.5 mm; upper incisors less proodont or vertical; alveolar process on the lingual wall of the mandibular ramus is feeble ……………………………………….…....... *lusitanicus*

11a) Present in the Italian Peninsula; NF$_a$=58 …… 12

11b) Present in the Balkan Peninsula; NF$_a$≤54 ….. 14

12a) Endemic to Sicily; 6 plantar pads and 6 nipples ……………….. *nebrodensis*

12b) Present in Peninsular Italy; 5–6 plantar pads and 4–6 nipples but not in a combination of 6 pads and 6 nipples ……………………………..………..... 13

13a) Present mainly to the west of the 14th meridian; X chromosome is metacentric ………….……......….. *savii*

13b) Present mainly to the east of the 14th meridian; X chromosome is submetacentric or acrocentric ………………………….................…… *brachycercus*

14a) TL/H&B<0.24; incisors strongly proodont; skull deep, braincase squarish; M^3 usually without postero-lingual re-entrant angle LR4; 2n≤44 ………..... *thomasi*

14b) TL/H&B >0.24; incisors less proodont or vertical; skull shallower, braincase rectangular; M^3 frequently has postero-lingual re-entrant angle LR4; 2n=54 …...….. *felteni*

Species group *majori*

Taxonomy. This species group with *majori* as the only species, is putatively basal in the subgenus (Tougard 2017); Jaarola et al. (2004) suggested a sister position of *majori* against the *subterraneus* group. *M. majori* was frequently regarded as a close relative of *subterraneus* and *daghestanicus* or their senior synonym, or was aligned with *schelkovnikovi* (Pavlinov & Rossolimo 1987). Based on chromosomal evidence, Kuliev & Bickham (2010) proposed a taxonomic split in *majori*, advocating for the status of independent species for *ciscaucasicus* and *suramensis*.

In the Caucasus, *majori* and *daghestanicus* are broadly sympatric but do not hybridise in nature (Baskevich et al. 1984). Interspecific hybrids produced in captivity were partly (females) or entirely sterile (males) (Malygin et al. 2000).

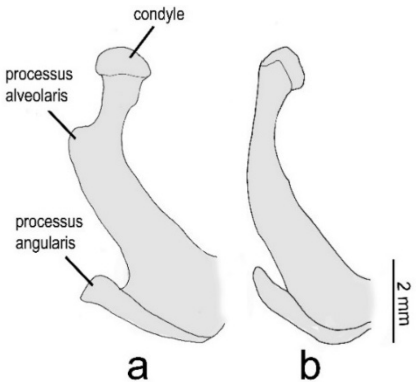


Figure 264: Caudal view of left ramus mandibulae in *Microtus duodecimcostatus* (a–Algeciras, Spain) and *M. lusitanicus* (b–Linares de Riofrio, Salamanca, Spain).

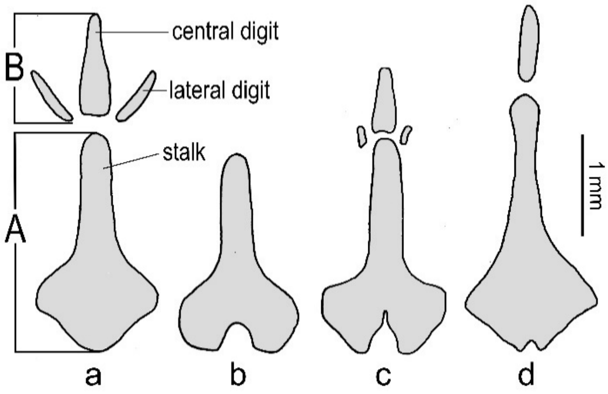


Figure 265: Shape of baculum in pine voles: a,b–*M. subterraneus* (Mt. Pelister, North Macedonia); c–*M. savii* (Maiella Mts., Italy); d–*M. thomasi* (near Trebinje, Bosnia and Herzegovina) ; A–proximal baculum; B–distal baculum (trident).

Microtus majori (Thomas, 1906) – Major's Pine Vole

Microtus (Pitymys) Majori Thomas, 1906b:419. Type locality: "Sumela [= Meryemana]", south of Trabzon, Turkey.

Synonyms. *M[icrotus] Dinniki* Satunin, 1903 [nomen nudum]; *Microtus (Arb[usticola]) rubelianus* Shidlovskiy, 1919; *M[icrotus] (Arb[usticola]) rubelianus colchicus* Shidlovskiy, 1919; *Arbusticola rubellianus ciscaucasicus* Ognev, 1924; *Arbusticola rubellianus Vinogradovi* Sviridenko, 1936 [nomen nudum]; *Microtus majori labensis* Heptner, 1948 [new name for *vinogradovi* Sviridenko 1936]; *P[itymys] m[ajori] transcaucasicus* Khatukov & Tembotov, 1982 [preoccupied by *Microtus arvalis transcaucasicus* Ognev 1924].

Distribution. (Figure 266). Endemic to the Greater and Lesser Caucasus and the eastern Pontic mountains; the range covers 162,650 km². Present in cis-Caucasian Russia (Krasnodar, Stavropol', Adygeya, Kabardino-Balkariya, Karachayevo-Cherkesiya, North Ossetia, marginally in Chechnya), throughout Georgia, sporadically in northern and south-western Azerbaijan, northern Armenia, and north-eastern Turkey (Artvin, Giresun, Ordu, Rize, and Trabzon). Earlier reports for Europe related to *subterraneus* (Kryštufek et al. 1994). Putative presence in Iran (Gromov & Erbajeva 1995) requires confirmation. Major's pine voles occupy humid clearings and forest edges in the zone of broadleaved and mixed forests (Lavrova & Barsova 1969, Kryštufek & Vohralík 2005) from sea level up to 2,660 m.

Characteristics. A large pine vole with a comparatively long tail (TL/H&B=0.35–0.45). Dimensions: BWt=20–29 g, H&B=90–112 mm, TL=32–49 mm, HF=15.5–17.6 mm, EL=9–12 mm,

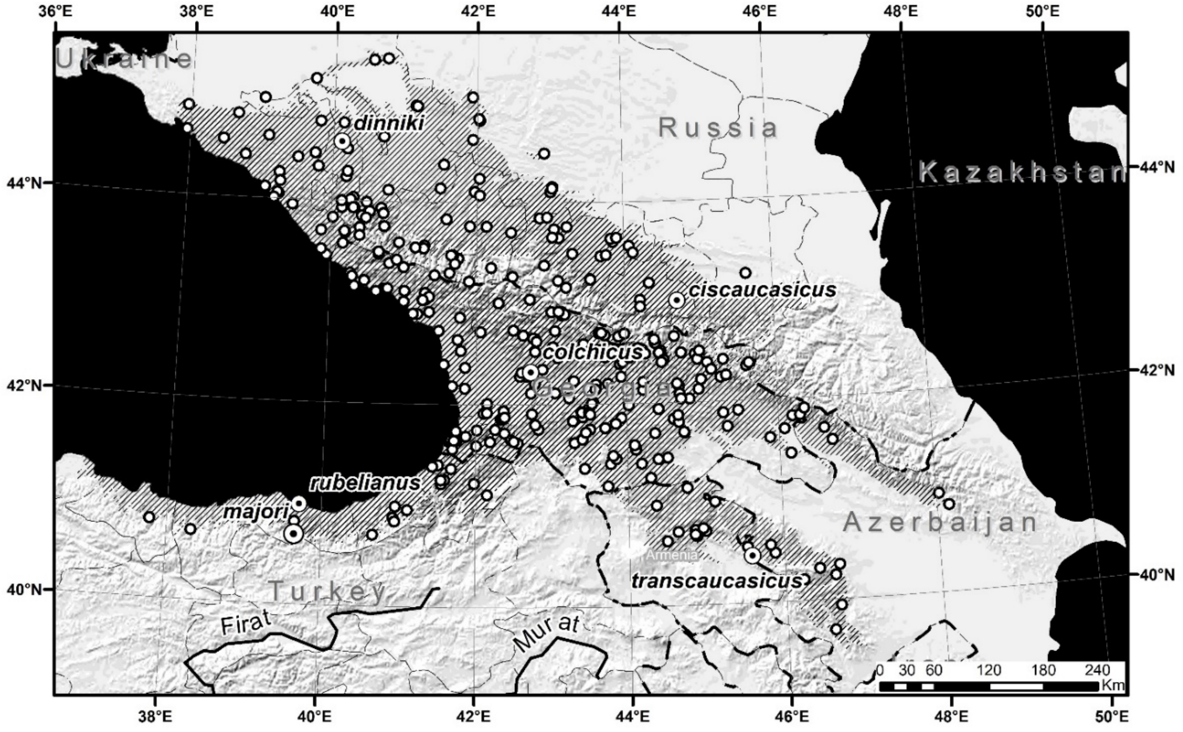


Figure 266: Distributional range of Major's pine vole *Microtus majori*.

CbL=22.5–24.9 mm, ZgW=12.8–15.6 mm, MxT=5.7–6.7 mm (Kryštufek & Vohralík 2005). Pelage is dark, mummy-brown above, slaty-grey below; the tail is indistinctly bi-coloured, blackish-brown above, dull whitish below and growing darker towards the tip. Feet are dull whitish. Females have 3 pairs of nipples (2 inguinal and 1 pectoral pair, respectively). Glans penis is 10 mm long and 2.5 mm wide with a small notch at the tip (Çolak et al. 1998). Baculum is of standard trident type: the proximal bone is 2.05–2.60 mm long and 1.15–1.55 mm wide across the basal expansion (Aksenova 1983). Head of sperm is elongated and rather small; length=5.6–6.7 μm, width=2.1–2.9 μm (Baskevich 1997). The skull is deep with normally expanded zygomatic arches (ZgW/CbL=56–63) and a wide interorbital region; the dorsal profile is either flat or convex but not depressed (Figure 267). Incisors are orthodont. Molars: M^3 normally has 4 inner and 3 outer salient angles (rarely up to 5 inner and 2–5 outer salient angles; Angermann 1974); dental fields of T2–T3 are confluent. In ~⅓ of cases, M^2 has postero-lingual salient angle LS4 but its dental field remains open (closed in ~2% of individuals); LS4 is more rarely (~8%) present in M^1 and is never closed (Angermann 1974). M_1 is rather robust with 5 inner and 4 outer re-entrant angles; BR4 and LR5 are usually shallow, leaving a wide isthmus connecting the anterior cap with posterior dental triangles T6–7; salient angles LS6 and BS5 are usually prominent and directed backward, thus giving the cap a symmetrical mushroom shape (Figure 268).

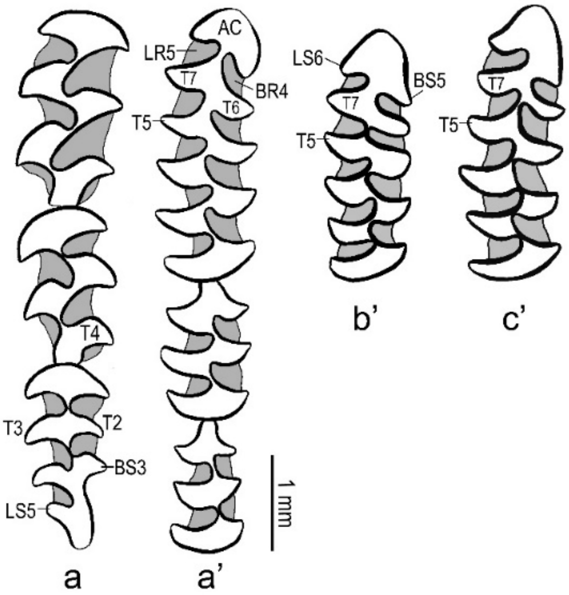


Figure 268: Enamel molar pattern in Major's pine vole *Microtus majori*: upper (a) and lower row (a'– near Murgul, Artvin, Turkey); isolated M_1 from Cankurtaran Geçidi, Artvin (b'), and Meryemana, Trabzon, Turkey (c').

Variation and subspecies. Several authors (Ognev 1950, Gromov et al. 1963, Gromov & Erbajeva 1981) recognised 3 loosely defined subspecies (*majori*, *suramensis* and *ciscaucasicus*), and Gromov & Baranova (1981) added *vinogradovi*.

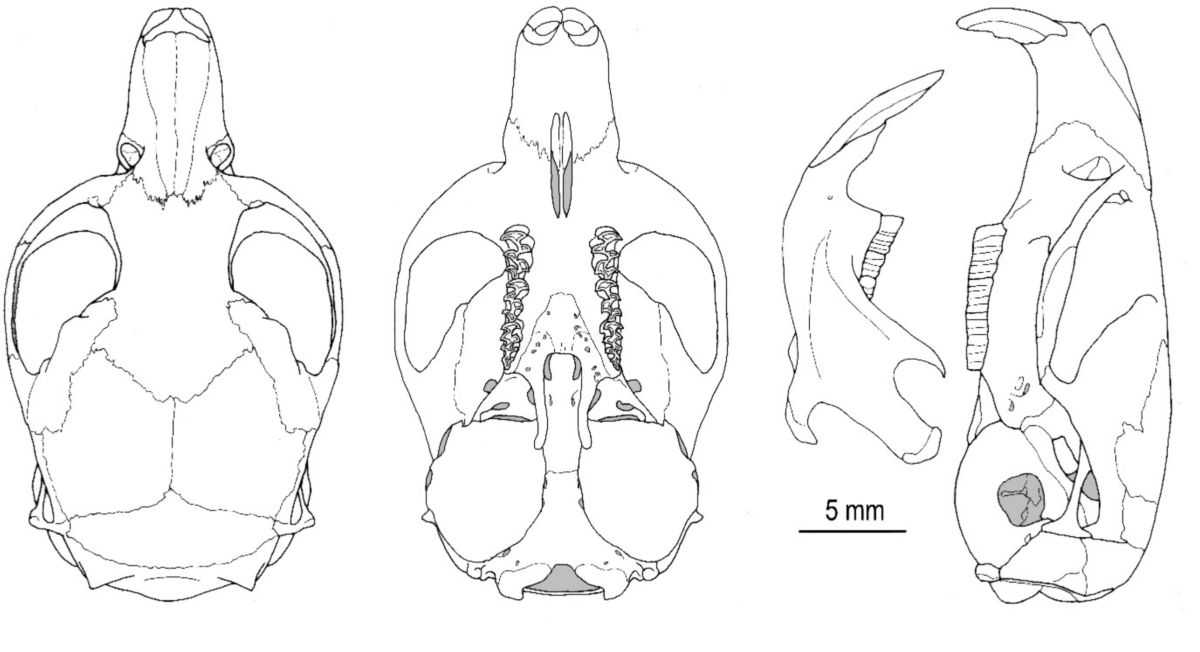


Figure 267: Skull in Major's pine vole *Microtus majori* (Meryemana, south of Trabzon, Turkey).

Species group *subterraneus*

Taxonomy. In the past the *subterraneus* group embraced *schelkovnikovi* (subgenus *Microtus*) and all pine voles with a complex M^3, which are now in the *majori* and *multiplex* groups. The number of recognised species in the group was either a single one (i.e. *subterraneus*; e.g. Ellerman & Morrison-Scott 1951) or two (also *daghestanicus*; e.g. Kryštufek & Vohralík 2005); recognition of *fingeri* as a species in its own right is a novel view. Macholán et al. (2001) suggested that *subterraneus* is paraphyletic with respect to *majori* and *daghestanicus* which has not been confirmed in subsequent studies.

Distribution. Caucasus, Asia Minor, and Europe between the Atlantic coast of France and the Volga River.

Characteristics. Small to moderately large pine voles with a comparatively short tail, large ears and tiny eyes; there are 2–3 pairs of nipples and 5 (rarely 6) plantar pads. The skull is low; M^3 usually has 4 inner and 3 outer salient angles and M^2 tends to have an imperfect postero-lingual loop LS4. Sperm head is larger and comparatively wider than in *majori.*

Microtus subterraneus (Sélys, 1836) – European Pine Vole

Arvicola subterraneus Sélys, 1836:10. Type locality: "Waremme, Liége, Belgium" (Miller 1912a:758).

Synonyms. *Agricola microtus* Gérard, 1871 [nomen nudum]; *[Arvicola agrestis] fusca* Fatio, 1900; *Pitymys subterraneus capucinus* Miller, 1908; *Pitymys dacius* Miller, 1908; *Pitymys ukrainicus* Vinogradov, 1922; *Pitymys zimmermanni* Matschie, 1924; *Pitvmys transsylvanicus* Éhik, 1924; *Pitvmys kupelwieseri* Wettstein, 1925; *Pitymys multiplex Brauneri* V. Martino & E. Martino, 1926; *Pitymys subterraneus Wettsteini* Éhik, 1926; *Pitymys dacius hungaricus* Éhik, 1926; Pitymys *incertoides* Wettstein, 1927; *Pitymys ehiki* Wettstein, 1927; *Pitymys subterraneus matrensis* Éhik, 1930; *Pitymys nyirensis* Éhik, 1930; *Pitymys subterraneus atratus* Stein, 1931; *Pitymys nyirensis martinoi* Éhik, 1935; *Pitymys mustersi* V. Martino & E. Martino, 1937; *Pitymys multiplex hercegoviniensis* V. Martino & E. Martino, 1940; *Pitymys Klőzeli* Éhik, 1942; *Pitymys dacius neuhauseri* V. Martino & Paspalev, 1956; *Pitymys subterraneus transvolgensis* Schaposchnicov & Schanev, 1958; *Microtus (Pitymys) subterraneus serbicus* Kretzoi, 1958 [new name for *Pitymys multiplex brauneri* V. 0Martino & E. Martino, 1926 (preoccupied by *Microtus arvalis brauneri* V. Martino & E. Martino 1926)]; *Microtus (Pitymys) dinaricus* Kretzoi, 1969 [new name for *Pitymys mustersi* V. Martino & E. Martino (preoccupied by *Microtus mustersi* Hinton, 1926)]; *P[itymys] sub[terraneus] dinaricus* Petrov, 1992 [nomen nudum]; *P[itymys] sub[terraneus] neglectus* Petrov, 1992 [nomen nudum]; *P[itymys] sub[terraneus] subterraneoides* Petrov, 1992 [nomen nudum].

Taxonomy. The taxonomic scope of *subterraneus* has gradually stabilised since the 1980s (Niethammer & Krapp 1982, Baskevich 1997). Prior to this, *schelkovnikovi* and up to 5 currently recognised pine vole species with a complex M^3 (*majori, daghestanicus, fingeri, multiplex*, and *liechtensteini*) were synonymised with *subterraneus.*

The identity of *Pitymys multiplex Brauneri* V. Martino & E. Martino was repeatedly challenged over the last decades. Topotypes from Mt. Prenj (Bosnia and Herzegovina) have 50 somatic chromosomes and therefore belong to *subterraneus* (Petrov & Živković 1979). Subsequently Petrov (1992) synonymised *hercegoviniensis* with *multiplex,* though providing no new evidence. We examined museum vouchers from Bosnia and Herzegovina in the Natural History Museum London (including the type of *hercegoviniensis*), Zoological institute in St. Petersburg (Martino's collection, including 1 paratype of *hercegoviniensis*), and the Slovenian Museum of Natural History (Petrov's collection, including the karyotyped topotypes of *hercegovinensis*). We conclude that they are all *subterraneus.* Corbet (1978:108) concluded that "The holotype of *P. m. hercegoviniensis* Martino, 1940 appears to be a mismatched skin of a *Pitymys* [*Terricola*] and a skull of *Microtus.*" In a vial with the skull of the type we found Corbet's hand-written note: "skull possibly *Microtus agrestis*". We assume that Corbet was misled by the postero-lingual salient angle LS4 (T5) which is prominent in the type of *hercegoviniensis.* The type however shows all the essential characteristics of

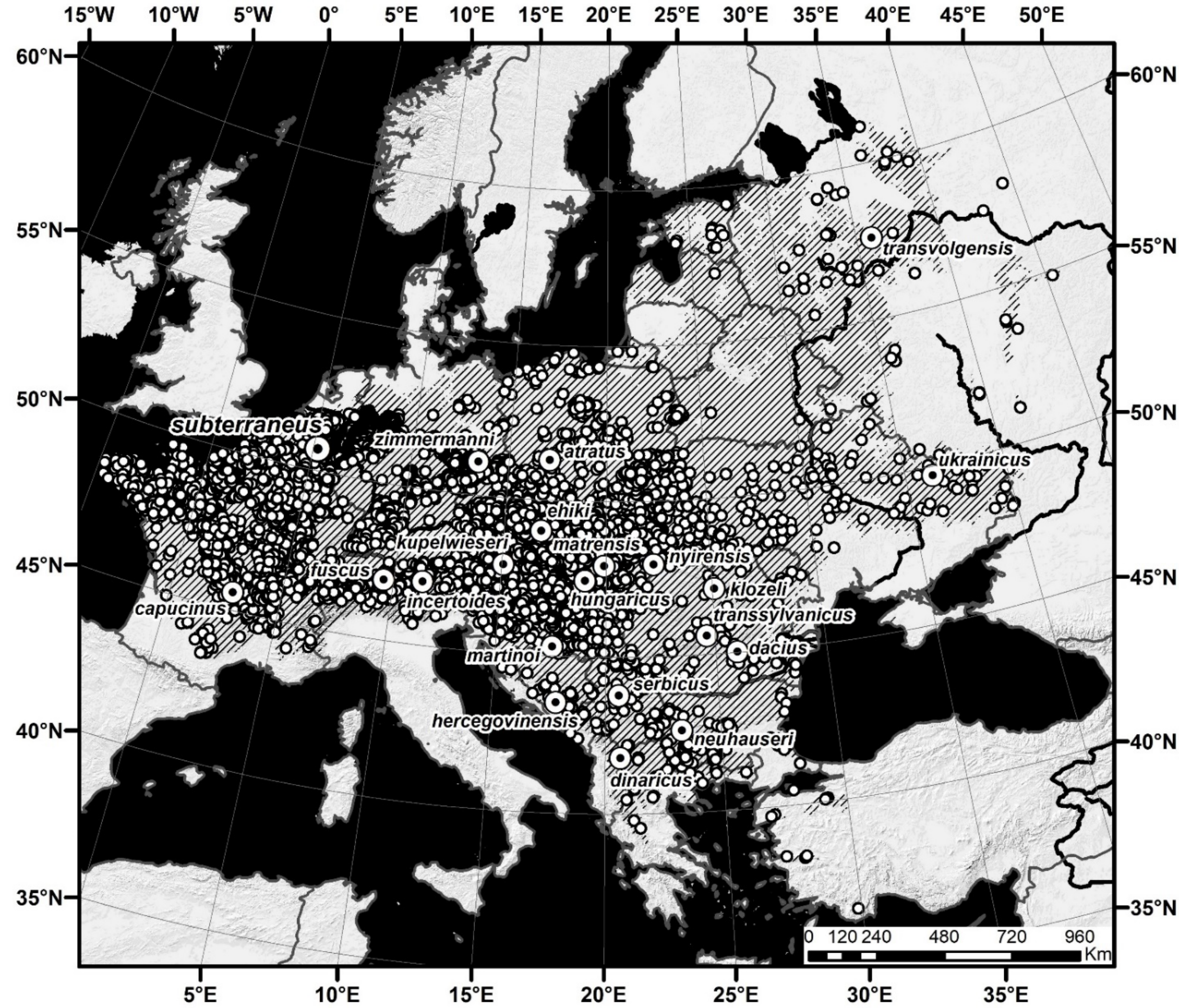


Figure 269: Distributional range of the European pine vole *Microtus subterraneus*.

subterraneus: a rather low skull with a broad and flat interorbital region and the M_1 with confluent dental fields T4–T5.

Distribution (Figure 269). The area (=3,181,935 km^2) is larger than for any other *Terricola* vole. *M. subterraneus* is common throughout France (except in the south and south-west), in the Low Countries and in Germany (absent from the North Sea Coast and Denmark); widespread through Central Europe and the Alps (the Czech Republic, Slovakia, Switzerland, Austria, northern Italy, Hungary, Poland) but absent from the Italian Peninsula. It is widespread in south-eastern Europe (Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, Albania, Serbia, North Macedonia, northern Greece, Bulgaria, Romania, Moldova) although it is mainly absent from the coastal areas and the lowlands of Thrace. In Ukraine, the European pine vole is still widespread except in the southern lowlands (south of Dnipropetrovsk) and in Crimea. The animal is less abundant in the rest of Eastern Europe where the range is also more fragmented. Records are scarce in Belarus, Latvia and Estonia, with none available from Lithuania. In northern Russia, records of occurrence are still reasonably common between the upper Volga and the Lakes of Ladoga and Onega as far east as the 45th meridian. In the vast lowlands of western Russia between the Dnepr and the Volga, localities are few and are widely scattered. The species was already rare in Eastern Europe during the Pleistocene (Krokhmal & Rekovets 2010). *M. subterraneus* is also present in Western Anatolia from Mt. Uludağ above the city of Bursa to the Bey Dağları Mts. west of Antalya.

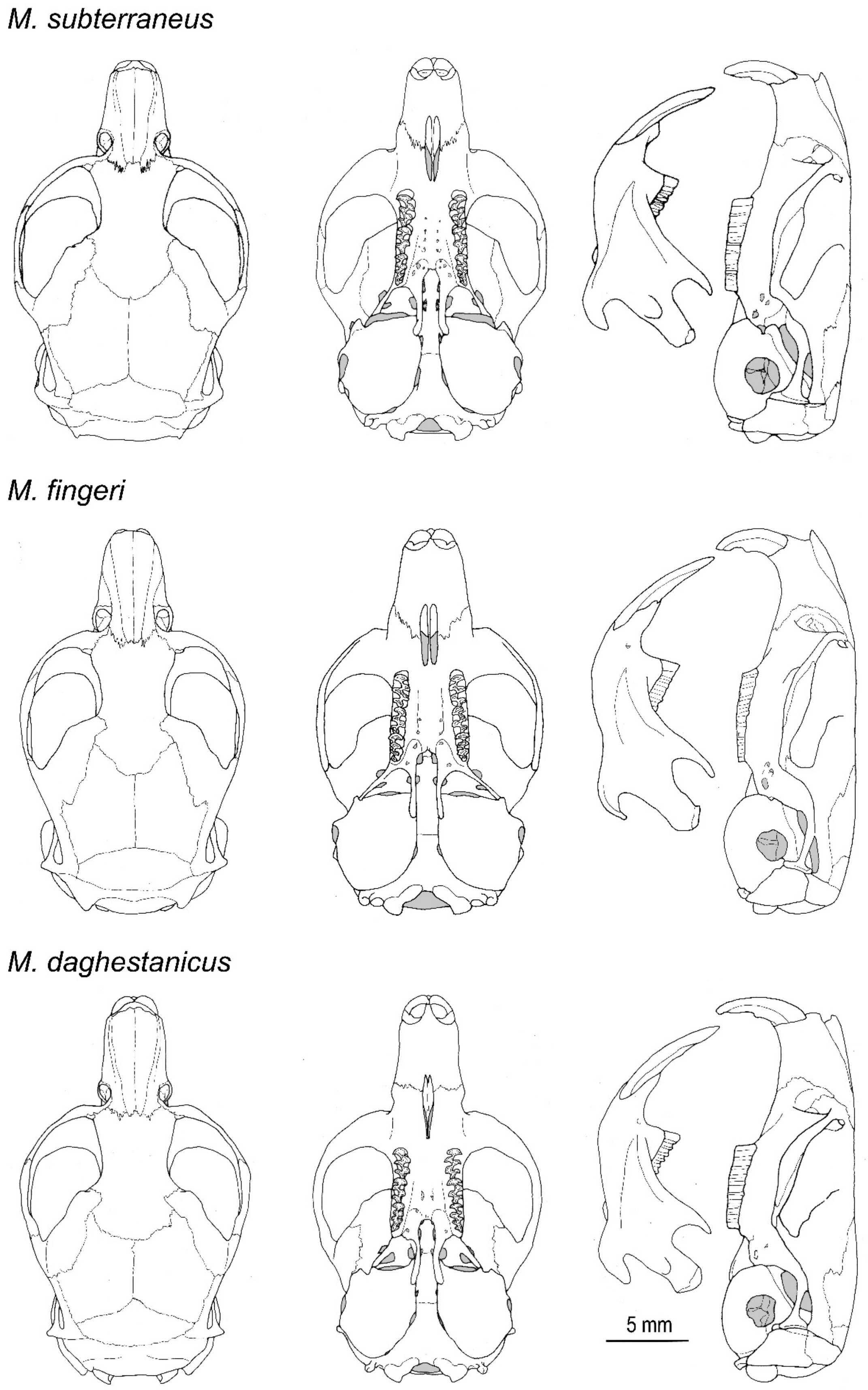


Figure 270: Skull in pine voles of the *subterraneus* species group: top–*Microtus subterraneus* (Lake Matty, Hungary: top); middle–*M. fingeri* (Tamdere, Giresun, Turkey); bottom–*M. daghestanicus* (Ovitdağ Pass, south of Rize, Turkey).

The European pine vole was reported from a wide range of habitats: small-scale cultivations, early successional stages in deciduous and coniferous forests, alpine meadows and rocky outcrops. Moist and disturbed situations with dense herbaceous vegetation are preferred. Altitudinal range is between sea level and 2,660 m. Although its range overlaps several other pine voles (*pyrenaicus, multiplex, liechtensteini, tatricus*, *felteni)*, syntopic occurrences of 2 pine vole species are rare.

Characteristics (Figure 262a,b). Dimensions: BWt=10–30.5 g, H&B=84–110 mm, TL=20–39 mm, HF=12–17 mm, EL=7–11 mm, CbL=21.4–24.2 mm, ZgW=12.4–14.8 mm, MxT=5.3–6.4 mm. Small to medium-sized pine vole with large ears and tiny eyes (diameter ≤2 mm; Kratochvíl 1964) and a moderately long tail (TL/H&B=0.20–0.36). Fur is soft, long (length=7–8.5 mm in summer pelage) and dense; protruding hairs are longer by 1–1.5 mm; tail annulation is not fully clad and terminal pencil is weak (length=1–1.8 mm). Back is uniformly brown, brownish buff, or dark brown; grey belly frequently has a buff or cream shade. There is no sharp demarcation along flanks. Tail is bi-coloured (brown above, grey below) and feet are greyish or brownish. Females have two pairs of inguinal nipples; an additional pectoral pair is rare (Kryštufek et al. 1994). Glans penis (length=10 mm, width=2.3 mm) is of simple cylindrical shape (Çolak et al. 1998). The baculum is of typical arvicoline trident structure; the stalk is 2.05–2.30 mm long and 1.05–1.20 mm wide at the base; the proximal margin of the base is of variable shape, usually with a protrusion and occasionally with a notch (Figure 265a,b). The central and lateral distal digits measure 0.95–2.0 mm and 0.45–0.8 mm, respectively (Hrabě 1972). The sperm head is 6.2–7.4 μm long and 2.8–3.7 μm wide (Baskevich 1997).

The skull is shallow with moderately expanded zygomatic arches (ZgW/CbL=0.56–0.62). The dorsal profile is nearly straight. Rostrum is relatively weak while the braincase is comparatively large; bullae are moderately swollen (Figure 270). Mandible is slender and low and lacks a prominent bulge at the alveolar process. The upper incisors are strongly curved and orthodont. M^3 has 4 (rarely 3) inner and 3 (rarely more) outer salient angles; dental fields T4–T5 are confluent in ~90% of molars. M^2 shows a tendency toward the presence of an imperfect postero-lingual loop (LS4) which is obvious in ~½ of molars; the loop may be prominent but is rarely entirely closed (~5% of individuals from central Europe; Angermann 1974). M_1 has 5 inner and 4 (rarely 5) outer re-entrant angles. Triangles T6–T7 are confluent and usually broadly communicate with the anterior cup; in rare cases

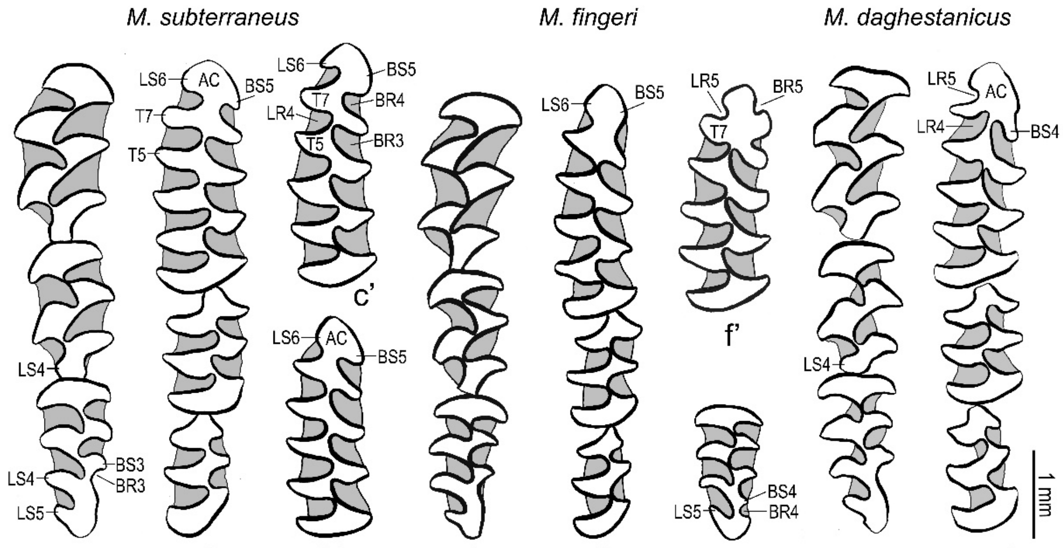


Figure 271: Molar pattern in pine voles of the *subterraneus* species group. *Microtus subterraneus*: upper (a) and lower row (a'–near Belgrade, Serbia); isolated M_1 from Balikli, Istanbul (b') and Cığlıkara, Antalya, Turkey (c'). *M. fingeri*: upper (d) and lower row (d'–east of Güzyurdu, Erzurum, Turkey); isolated M^3 (e–Güzyurdu) and M_1 (f'–Abant Lake, Bolu, Turkey). *M. daghestanicus*: upper (g) and lower row (g'–Dilijan, right bank of Aghstafa River, Armenia).

(~5%), deep re-entrant angles BR4 and LA5 isolate the cap. The anteroconid complex is long relative to the trigonid-talonid complex (Figure 271a-c').

Karyotype is polymorphic: 2n = 52 or 54; the fundamental number of arms is constant (NF_a=56). The X chromosome is medium to large bi-armed, the Y is usually acrocentric of varying size (Sablina et al. 1989, Baskevich et al. 2000, Arslan & Zima 2014). Chromosomal polymorphism (see below) is an intraspecific phenomenon, although heterozygotes may be selectively disadvantageous (Meylan 1972).

Variation and subspecies. A large number of subspecific names is available but "most of subspecies can not be really distinguished" (Shenbrot & Krasnov 2005:254). Geographic structuring is weak, possibly the result of rapid radiation and simultaneous diversification of many lineages coupled with limited gene flow. The 2 cytotypes show a geographic pattern: the 2n= 52 form is contiguously present in central and south-eastern Europe, while the 54-cytotype occupies the periphery in Belgium, Switzerland, Germany, north-eastern Poland, Russia, and Anatolia (Sablina et al. 1989, Arslan & Zima 2014). Zagorodnyuk (1990, 1993) ranked these cytotypes as distinct species, *subterraneus* (2n=54) and *dacius* (2n=52). Pine voles from the southern Balkans tend to be larger (Kryštufek et al. 1996). Life history traits show a latitudinal cline (Zagorodnyuk 1992).

Microtus fingeri (Neuhäuser, 1936) – Anatolian Pine Vole

Pitymys majori fingeri Neuhäuser, 1936a:159. Type locality: "Karadere, north of Bolu", Turkey.

Taxonomy. *M. fingeri* has thus far been held in synonymy of *majori* and afterwards of *subterraneus*. We rank it as a species in its own right on the basis of a deep divergence in *Mt*-sequences (Bogdanov et al. 2021; our unpublished results).

Distribution (Figure 272). The range covers a rather small area (73,805 km²) in northern Anatolia (Turkey) and stretches in a narrow belt along the Black Sea coast from the eastern shore of the Sea of Marmara to Gümüşhane. The classification of voles from Tatvan as *fingeri* is tentative. Habitat preferences are similar to the European pine vole; altitudinal range is 70–2,000 m. *M. fingeri* is seemingly allopatric with respect to *subterraneus* and *daghestanicus*.

Characteristics. Dimensions: BWt=13–25 g, H&B=87–110 mm, TL=28–44 mm, HF=14–17 mm, EL=7.2–11.5 mm, CbL=21.4–25.0 mm, ZgW=12.2–

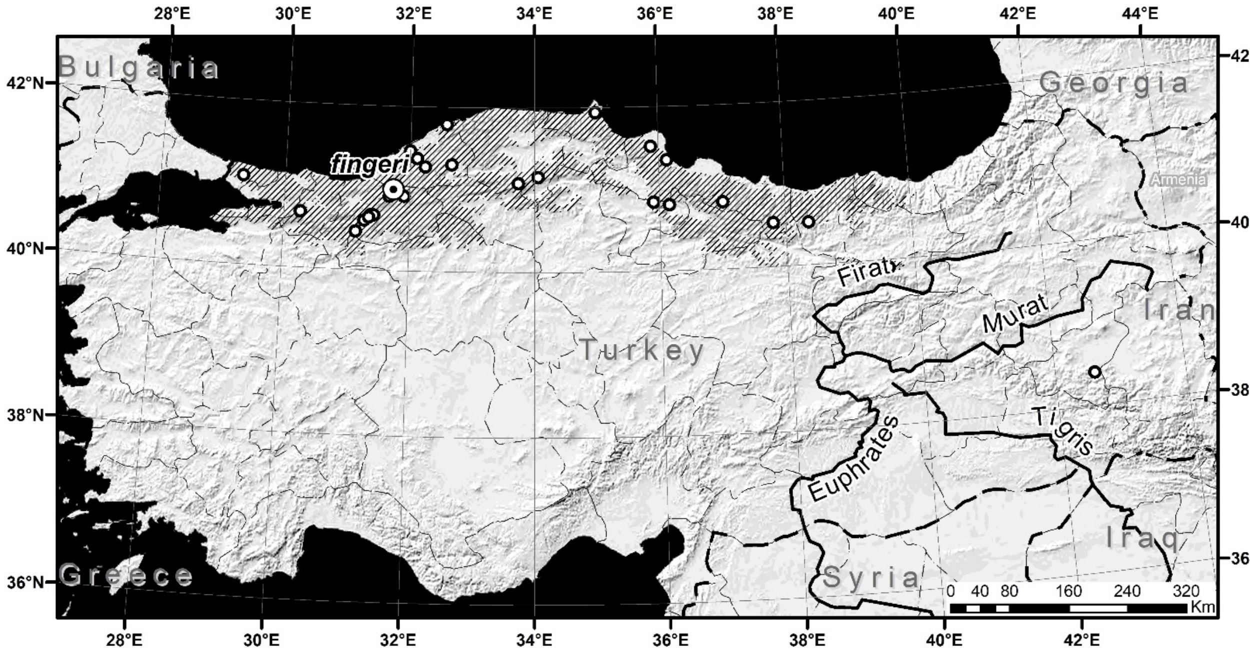


Figure 272: Distributional range of the Anatolian pine vole *Microtus fingeri*.

14.7 mm, MxT=5.2–6.4 mm. Similar to *subterraneus* in all aspects of external morphology including glans penis and baculum (Çolak et al. 1998). Skull is slightly shallower and the dorsal profile may be concave in the orbital region (Figure 270) like in *daghestanicus*. The orbital region is on average more constricted. Molars are as in *subterraneus* (Figure 271). Karyotype: 2n=54, NF$_a$=56; the X chromosome is large submetacentric (Macholán et al. 2001).

Variation and subspecies. Monotypic. Size declines in a west-to-east direction; a decline is particularly obvious in the M$_1$ length which measures 2.59–2.94 mm in the west and 2.22–2.63 mm in the east (Kryštufek & Vohralik 2004).

Microtus daghestanicus (Shidlovskiy, 1919) – Dagestan Pine Vole

M[icrotus] (Arb[usticola]) rubelianus daghestanicus Shidlovskiy, 1919:12. Type locality restricted to "Karda (Gunibskiy okrug [District], Dagestan", Russian Federation, by subsequent designation of the type (Shidlovskiy 1938:90).

Synonyms. *M[icrotus] (Arb[usticola]) rubelianus intermedius* Shidlovskiy, 1919 [status uncertain; possibly synonymous with *majori*]; *Pitymys (Arbusticola) daghestanicus nasarovi* Shidlovskiy, 1938; *Microtus majori suramensis* Heptner, 1948 [new name for *Microtus rubelianus intermedius* Shidlovskiy which is preoccupied by *intermedia* Bonaparte, 1845 (=*Microtus agrestis*)].

Taxonomy. *M. daghestanicus* was frequently synonymised with *majori* and rarely with *subterraneus*. Kratochvíl (1970) delimited *daghestanicus* from *majori* and *subterraneus*, and Ivanov & Tembotov (1972) provided supporting karyological evidence. The Dagestan pine vole is chromosomally polymorphic which prompted a taxonomic split into 2 species defined by a diploid number of chromosomes: 2n=52 or 54 in *daghestanicus* and 2n=38, 40 or 42 in *nasarovi* (Zima & Král 1984, Pavlinov & Rossolimo 1987, Kuliev & Bickham 2010). Cross-breeding of 2n=38

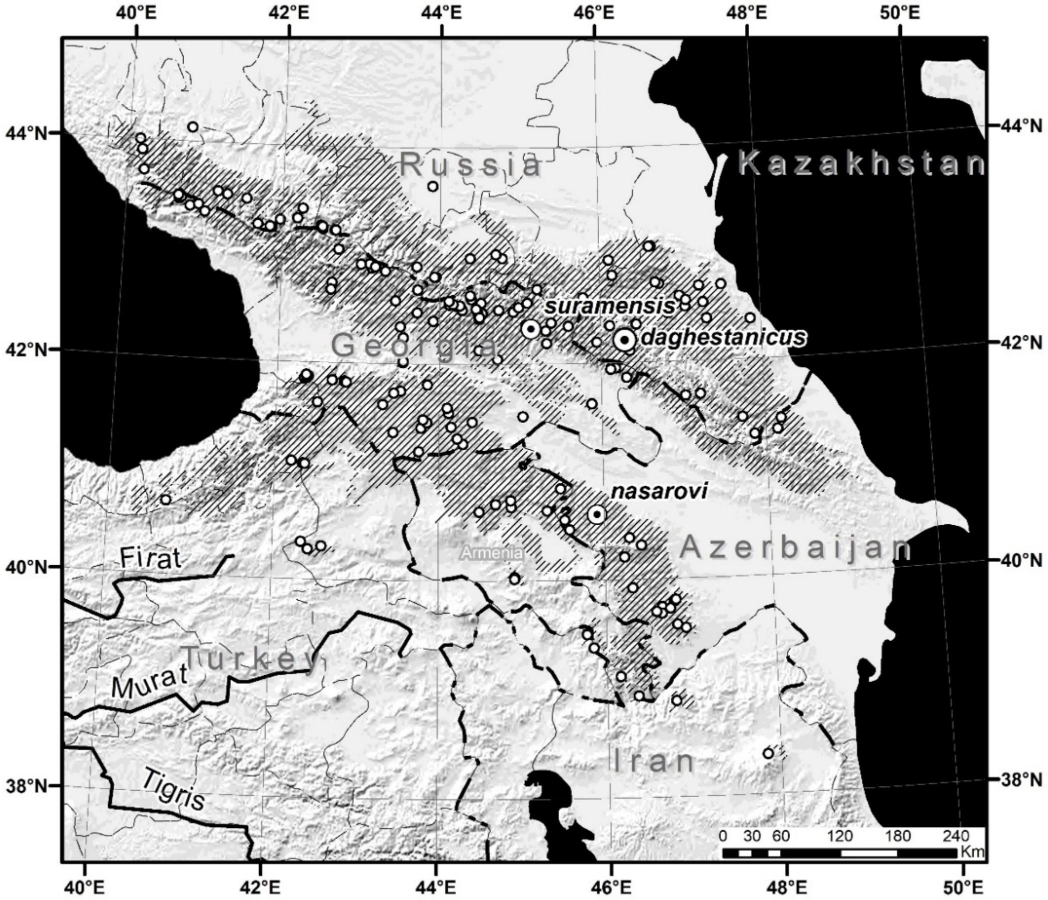


Figure 273: Distributional range of the Dagestan pine vole *Microtus daghestanicus*.

(*nasarovi*) and 2n=54 forms (*daghestanicus*) yielded sterile offspring (Zima & Král 1984).

Distribution (Figure 273). Endemic to the eastern and central Greater Caucasus in Georgia and Russia (Adygeya, Chechniya, Dagestan, Kabardino-Balkariya, Karachayevo-Cherkesiya, Krasnodar, and North Osetia) and in the Lesser Caucasus in Georgia, north-eastern Turkey (Ardahan, Artvin, Kars), Armenia, Azerbaijan (incl. Nakhichevan) and adjacent north-western Iran (Azarbayjan-e-Sharqi, and Ardabil). The range (area=124,000 km^2) broadly overlaps *majori*. The Dagestan pine vole inhabits alpine meadows and forest clearings at 235–2,900 m a.s.l.

Characteristics. Dimensions: BWt=15–25 g, H&B=81–105 mm, TL=29–42 mm, HF=13.7–16.4 mm, EL=9.5–12 mm, CbL=20.7–24.1 mm, ZgW=11.7–14.6 mm, MxT=4.8–6.3 mm. Externally similar to *subterraneus* except for having a slightly longer tail (TL/CbL=0.33–0.45), duller brownish-buff fur and 3 pairs of nipples (2 inguinal + 1 pectoral). Baculum shows no peculiarities, the basal stalk is 2.17 mm long and 1.37 mm wide (Kryštufek & Vohralík 2005). Glans penis is on average 3.4 mm long and 2.0 mm wide. The sperm head is of similar dimensions as in *subterraneus*: length=6.7–8.3 μm, width=2.8–3.6 μm (Baskevich 1997). Skull is lightly built and shallow; rostrum is on average longer than in *subterraneus* and the concave dorsal profile shows a depression in the orbital region (Figure 270). Zygomatic arches are moderately expanded (ZgW/CbL=0.59–0.63). Upper incisors tend to be more proodont than in *fingeri* and *majori*. Molars show no peculiarities (Figure 271).

Eleven cytotypes have been identified thus far: 2n=38, 40, 42 (2 subtypes), 43, 44, 45, 46, 52, 53, and 54; the fundamental number of chromosomal arms is stable NF_a=56 (Achverdjan et al. 1992, Baskevich et al. 2015). Achverdjan et al. (1992) reported the following hybrids: 42×44, 44×46, and 52×54.

Variation and subspecies. The major feature of interpopulation variation is chromosomal polymorphism. Only 1 cytotype (2n=54) is widespread; the 2n=52 cytotypes occurs in the northern slope of the Caucasus (Achverdjan et al. 1992) while the remaining are found to the south of the main Caucasian ridge in Armenia and Azerbaijan. No subspecies are recognised (Gromov & Erbajeva 1995, Shenbrot & Krasnov 2005).

Species group *savii*

Taxonomy. A monophyletic lineage restricted to the Apennine Peninsula. *M. savii* was long recognised as the only species in the group and occasionally contained a further 3 taxa with a simple M^3 pattern (*lusitanicus*, *pyrenaicus* and *felteni*). Restriction of *savii* proper to the Apennine Peninsula was followed by a stepwise split into 3 allopatric species (Bezerra et al. 2016). Taxonomic refinements, which were initiated by chromosomal research and hybridisation tests (Galleni et al. 1994, 1998), were followed a decade later by phylogenetic reconstructions (Castiglia et al. 2008). Two of these species (*savii* and *brachycercus*) produced sterile F1 males in captive trials (Galeni et al. 1994); no matching evidence is available for *nebrodensis*.

Morphological differentiation between the species is trivial and interspecific chromosomal differences are limited to sex chromosomes. Interspecific differentiation in heterosomes was accompanied by notable changes with regard to the number and locations of the rDNA sites; their number is high in *M. savii* (rDNA sites are present on 18 chromosomal pairs) and *M. nebrodensis* (13 pairs) but low in *brachycercus* (8–10 pairs; Gornung et al. 2011a). The evolutionary split between *savii* and *brachycercus* was putatively triggered by the amplification of heterochromatin (Galleni 1995). *M. nebrodensis* has the basal position in the phylogenetic tree of Savi's pine voles.

Distribution. Peninsular Italy and adjacent south-western Switzerland; also present on Sicily. Savi's voles are common along the edges of grassland and in forest clearings, preferably in damp and soft silicocalcareous terrain where subsoil is sufficiently deep for burrowing and lower strata permeable for rainwater; arid clay soils are avoided (Santini 1977).

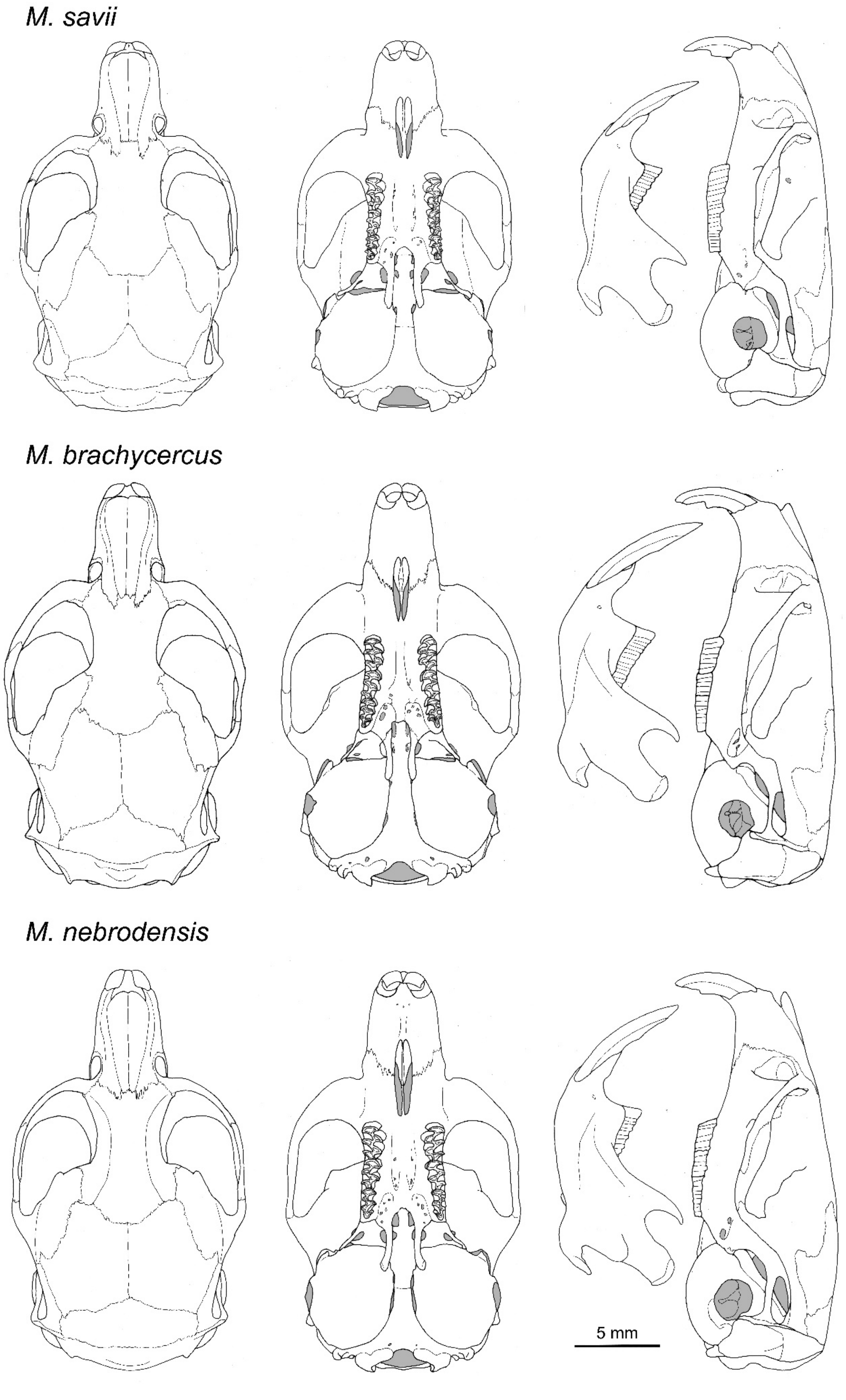


Figure 274: Skull in Savi's pine voles (top to bottom): top–*Microtus savii* (Maiella Mts., Italy); middle–*M. brachycercus* (Foresta Umbra, Monte Gargano, Italy); bottom–*M. nebrodensis* (Castelobuono, Sicily, Italy).

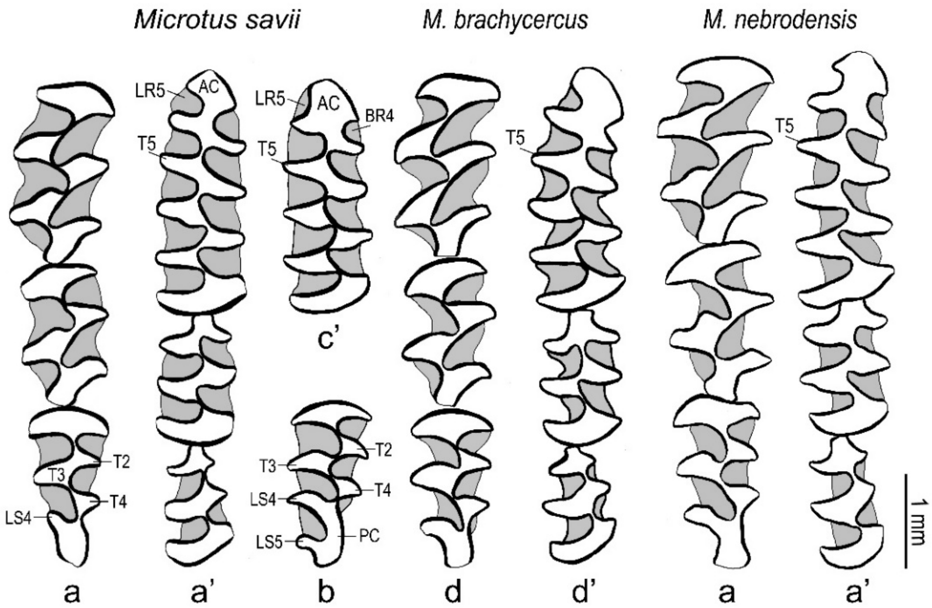


Figure 275: Molar pattern in Savi's pine voles. *Microtus savii*: upper (a) and lower row (a'–Marina di Pisa, Italy); isolated M^3 (b–Marina di Pisa) and M_1 (c'–Lago Trasimeno, Perugia, Italy). *M. brachycercus*: upper (d) and lower row (d'–Camiglia Letto, Calabria, Italy). *M. nebrodensis*: upper (e) and lower row (e'–Longo, Messina, Sicily, Italy).

Characteristics (Figure 262f). Small pine voles of the same external appearance as *M. subterraneus*. There are 5–6 small plantar pads (Figure 263); females have 2–3 pairs of nipples. Fur is soft and dense; dorsal side is brown, occasionally with buffy tints; the head may be duller; belly is grey and the transition along the flanks is usually obvious. Feet are whitish grey (never dusky); tail is light grey or whitish all around and slightly darker above. The skull is of average proportions (ZgW/CbL=0.58–0.64) and moderately deep; bullae are rather large (Figure 274). Upper incisors incline towards slight proodonty. M^1–M^2 show a tendency toward the presence of an imperfect postero-lingual loop. M^3 is short with 3 salient angles on either side. Additional posterior salient angle (LS5) is rarely present (<10% of individuals). The antero-labial triangle T2 is of normal size; dental fields of T2–T4 are frequently isolated; the posterior cap is short. The simple structure of M^3 is presumably an acquired characteristic rather than a primitive trait (Brunet-Lecomte et al. 1994). M_1 has a robust trefoil followed by triangles T4–T5 which form a transverse loop (Figure 275). The individual and regional variations blur interspecific differences in nearly all external, cranial and dental traits (Nappi et al. 2006, Piras et al. 2010). Karyotype: 2n=54; the autosomes are stable (NF_a=58), but sex chromosomes differ among and within species.

Microtus savii (Selys, 1838) – Common Savi's Vole

Distribution (Figure 276). Widespread in nearly all provinces of northern and central Italy, reaching the extreme south-west Switzerland in Ticino and Valais. Putative presence in the extreme south-east France (Louarn & Quéré 2003) requires confirmation (cf. Fayard 1984). In Italy, this pine vole spreads as far south as Abruzzo, Lazio, and the extreme west Molise. In northern Italy it has a marginal presence in Valle d'Aosta and Trentino-Alto Adige and is restricted to the southern parts of Lombardia and Veneto. The eastern border is on the Tagliamento River (Bon et al. 1995); further east, *M. savii* is known from a single locality in Friuli-Venezia Giulia (Amori et al. 2008). Distribution area covers 132,755 km^2 and the species is common from sea level up to 2,800 m (Nappi et al. 2006). Allopatric with respect to *brachycercus*.

Characteristics. Morphologically does not differ from the remaining 2 species of the group. There are 5–6 plantar pads; females have 2 pairs of (inguinal) nipples. Proximal baculum is 2.2 mm long; the base

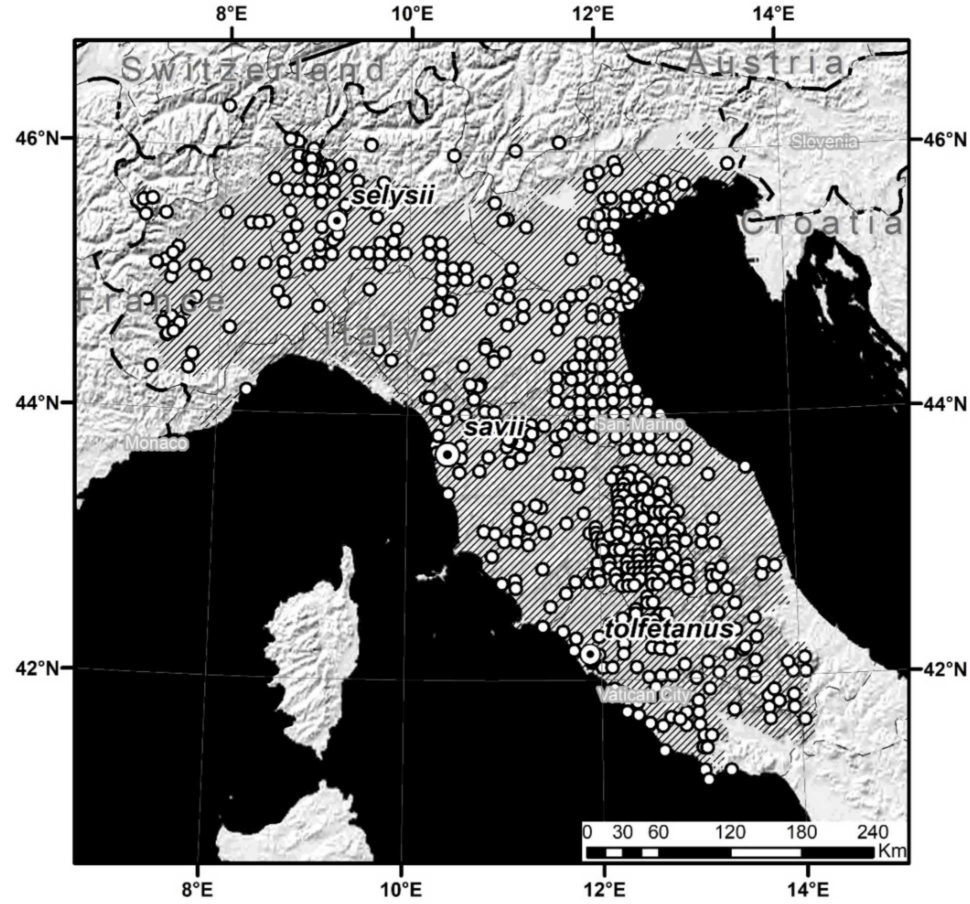


Figure 276: Distributional range of the common Savi's pine vole *Microtus savii*.

(width=1.25 mm) has a deep triangular notch (Figure 265c). Distal baculum is small, particularly the lateral digits; central digit is 0.65 mm long. Karyotype: 2n=54, NF_a=58; the Y chromosome is small acrocentric and the X chromosome is metacentic of medium size (Gornung et al. 2011a).

Variation and subspecies. Miller (1912a) recognised no subspecies. With 2 subspecies we follow Amori et al. (2008).

Microtus savii savii (Selys, 1838)

Arvicola Savii Selys, 1838:248. Type locality: "… la Toscane, la Lombardie et les environs de Genève." Restricted to "Neighbourhood of Pisa, Italy" (Miller 1912a:768).

Synonyms. *[Arvicola Savii]* Var. *albus* Lesson, 1842 [nomen nudum]; *[Arvicola Savii]* Var. *albomaculatus* Lesson, 1842 [nomen nudum]; *A[rvicola] Selysii* Bonaparte, 1845; *P[itymys] appenninicus* Major, 1909 [nomen nudum].

Distribution. Majority of the range of the species, except the Tolfa Mts.

Characteristics. Smaller: BWt=16–25.5 g, H&B=79–105 mm, TL=22–31 mm, HF=14–16.5 mm, EL=6.2–9.5 mm, CbL=21.1–24.5 mm, ZgW=12.2–15.2 mm, MxT=4.6–6.2 mm.

Microtus savii tolfetanus Contoli, 2003

Microtus (Terricola) savii tolfetanus Contoli, 2003:108. Type locality: "'La Fernesiana', Tolfa hills, Allumiere, Roma Province", Italy.

Distribution. Tolfa Mts. (Monti della Tolfa) and adjacent areas, northern Lazio, central Italy.

Characteristics. Larger: CbL=22.9–26.8 mm (Contoli 2003).

Microtus brachycercus (Lehmann, 1961) – Short-tailed Savi's Vole

Distribution (Figure 277). Endemic to southern Italy as far north as eastern Abruzzo and southern Lazio. The area of distribution covers $62,400 \text{km}^2$ and the species is common from sea level up to 1,855 m a.s.l.

Characteristics. Very similar to *M. savii*. Females have 2–3 pairs of nipples. Karyotype: 2n=54, $NF_a=58$; sex chromosomes are large due to the addition of heterochromatin. The Y is acrocentric and more than twice the size of that in *savii*; the X is either acrocentric or submetacentric (Galleni et al. 1994, 1998, Gornung et al. 2011a).

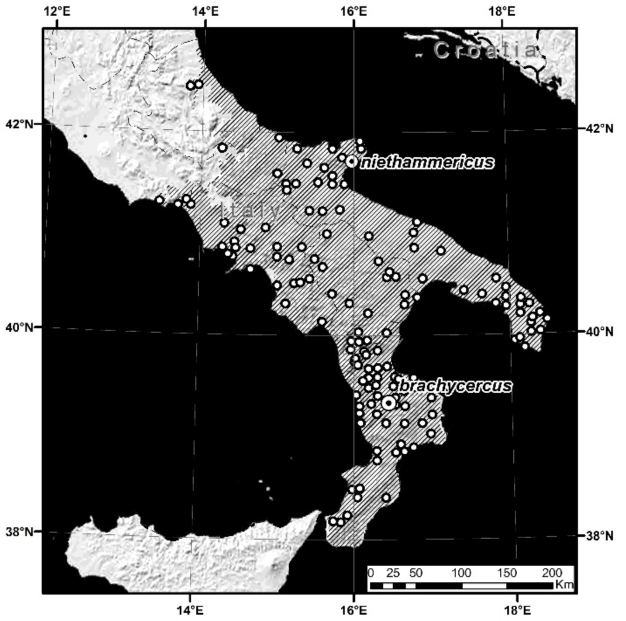


Figure 277: Distributional range of the short-tailed Savi's vole *Microtus brachycercus*.

Variation and subspecies. Subspecific taxonomy follows Amori et al. (2008).

Microtus brachycercus brachycercus (Lehmann, 1961)

Pitymys savii brachycercus Lehmann, 1961:223. Type locality: "Camigliatello Silano", Calabria, Italy.

Distribution. The majority of the range of the species, except Monte Gargano.

Characteristics. Females have 2 pairs of nipples (both are inguinal). The X chromosome is submetacentric (Gornung et al. 2011a). Dimensions: BWt=13.5–36 g, H&B=84–102 mm, TL=21–29 mm, HF=13–16 mm, EL=6–8.8 mm, CbL=21.2–23.4 mm, ZgW=12.6–14.3 mm, MxT=5.1–6.1 mm.

Microtus brachycercus niethammericus Contoli, 2003

Microtus (Terricola) savii niethammericus Contoli, 2003:109. Type locality: "'Forest Umbra' woodland and its surroundings (m.t Sant' Angelo etc.)". Lectotype is from "Foresta Umbra, 12 km in direction Monte San Angelo (41.13N 15.58E), 750 m, Monte Gargano, Italy" (Hutterer 2010:15).

Synonyms. *Microtus (Terricola) savii niethammeri* Contoli, 2000 [nomen nudum; not *niethammeri* Brunet-Lecomte & Volobouev, 1994 (see under *M. multiplex*)]

Taxonomy. Described by Niethammer (1981) and subsequently named as a new subspecies by Contoli (2003).

Distribution. Seemingly restricted to an isolated mountain massif of Monte Gargano, Province of Foggia.

Characteristics. Females have 3 pairs of nipples. The X chromosome is acrocentric (Niethammer 1981). Dimensions: BWt=14–24 g, H&B=78–89 mm, TL=20–27 mm, HF=13–16 mm, EL=6-5–8 mm, CbL=21.1–24.0 mm, ZgW=12.4–14.2 mm, MxT=5.4–6.2 mm.

Microtus nebrodensis (Minà-Palumbo, 1868) – Sicilian Savi's Vole

Arvicola Nebrodensis Minà Palumbo, 1868:61. Type locality: "slopes of Madonie", Sicily, Italy.

Taxonomy. Taxonomic status follows Bezerra et al. (2016).

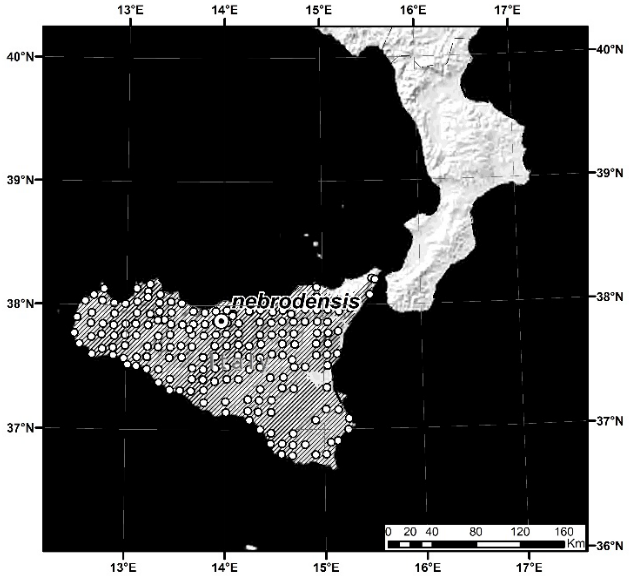


Figure 278: Distributional range of the Sicilian Savi's vole *Microtus nebrodensis*.

Distribution (Figure 278). Endemic to Sicily where widespread from close to sea level up to 1,905 m a.s.l. Distributional range covers 24,140 km^2.

Characteristics. As for the species group. There are 6 palmar pads and females have 3 pairs of nipples. Standard karyotype as in *savii*: 2n=54, $NF_a=58$ (Gornung et al. 2011a). Dimensions: H&B=84–102 mm, TL=22–29 mm, HF=15–16 mm, EL=10–11 mm, CbL=19.4–25.2 mm, ZgW=11.1–14.7 mm, MxT=4.9–6.4 mm.

Variation and subspecies. Monotypic.

Species group *duodecimcostatus*

Taxonomy. A monophyletic lineage of *Terricola* (Jaarola et al. 2004, Tougard 2017) restricted to the Iberian Peninsula and western France. Voles from the *duodecimcostatus* group were frequently split between the *savii* group (*pyrenaicus*) and the *duodecimcostatus* (or *ibericus*) group (*duodecimcostatus* and *lusitanicus*) (Miller 1912a, Chaline et al. 1988, Musser & Carleton 2005).

The number of recognised species was high in the early 20th century (e.g. 8 species in Miller 1912a) but was reduced to 2 species in the 1950s (Ellerman & Morrison-Scott 1951, Niethammer 1956).

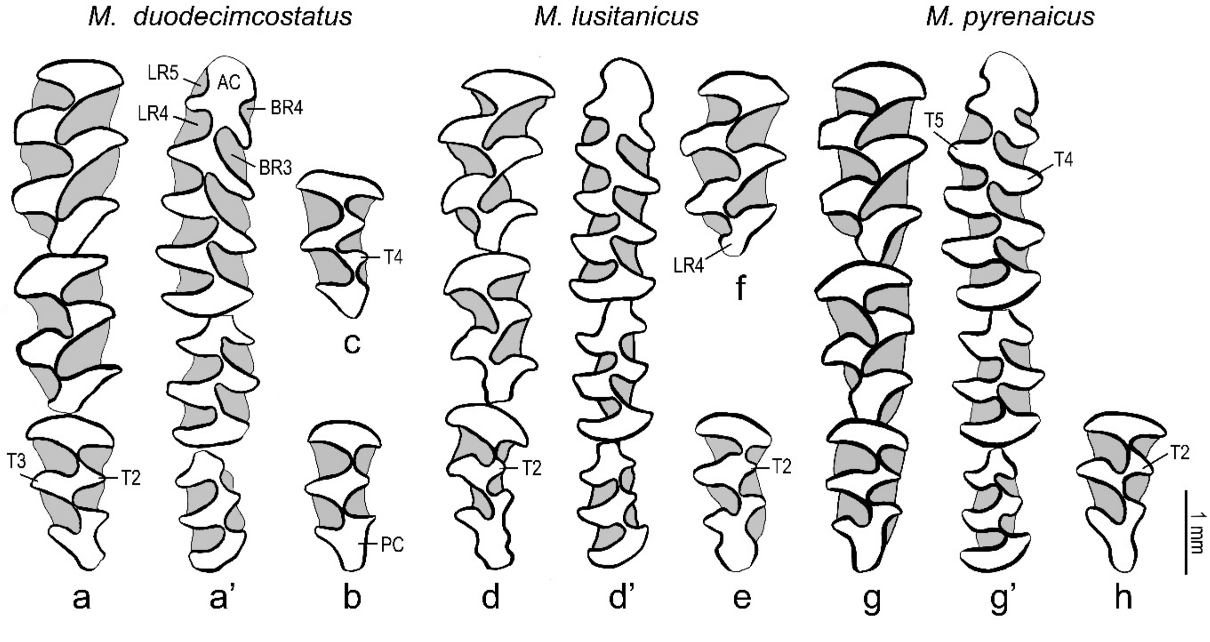
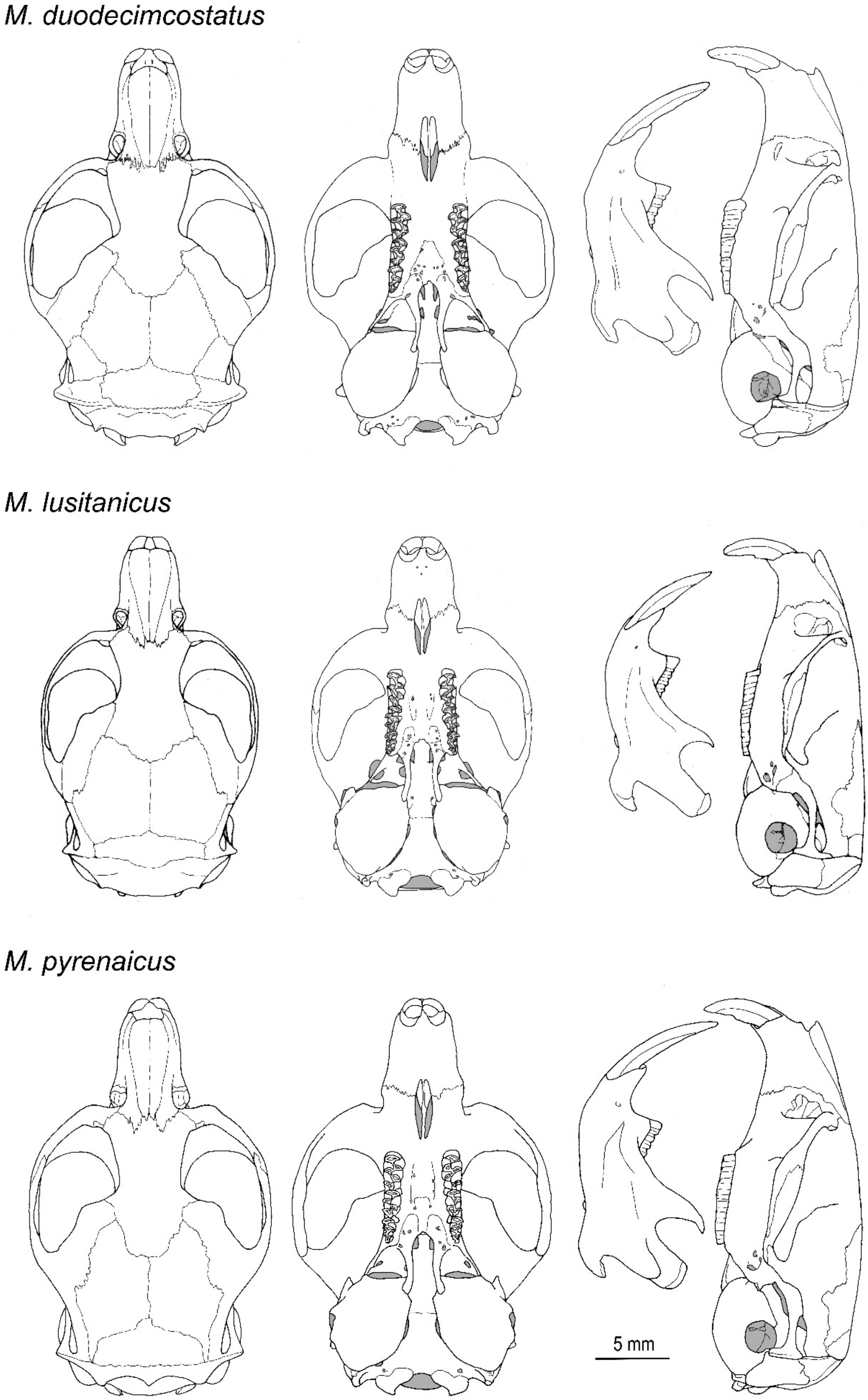


Figure 279: Molar pattern in pine voles of the *duodecimcostatus* species group. *Microtus duodecimcostatus*: upper (a) and lower row (a'–Bouches-du-Rhône, France); isolated M^3 (b–Bouches-du-Rhône; c–Algeciras, Spain). *M. lusitanicus*: upper (d) and lower row (d'–Linares de Riofrio, Spain); isolated M^3 (e) and M^1 (f–both from Salamanca, Spain). *M. pyrenaicus*: upper (g) and lower row (g'–Puente de Montanana, Spain); isolated M^3 (h–Provence, France).


M. duodecimcostatus

M. lusitanicus

M. pyrenaicus

Figure 280: Skull in pine voles of the *duodecimcostatus* species group: top–*Microtus duodecimcostatus* (Algeciras, Spain); middle–*M. lusitanicus* (Linares de Riofrio, Spain); bottom–*M. pyrenaicus* (Puente de Montanana, Spain).

Distribution. South-western Europe in France (south of the Loire Valley) and throughout Spain and Portugal. The range in the Iberian Peninsula does not overlap with other pine voles.

Characteristics. These voles possess 5 plantar pads and 2 pairs of inguinal nipples. The skull is moderately deep and usually shows a slightly bowed dorsal profile (Figure 279); upper incisors are orthodont or proodont with transitional stages connecting the extremes. M^1–M^2 show the tendency for the presence of an imperfect postero-lingual loop (LS3). M^3 is short with 3 salient angles on either side; an additional posterior loop which is occasionally present on the inner side is always shallow. The medial outer triangle T2 is normally rudimentary and confluent with T3; T4 widely opens into the posterior loop. M_1 has a robust trefoil anterior to a transverse loop formed by triangles T4–T5 (Figure 280).

Microtus duodecimcostatus (Sélys, 1839) – Mediterranean Pine Vole

Arvicola duodecimcostatus Sélys, 1839:8. Type locality: "banks of the Loire" (p. 9) where the species does not occur (Miller 1912a:784–785). Major (1905:508) claimed that the type originates from "the neighbourhood of Montpellier" which is accepted as the correct type locality ("Montpelier, Gard, Southern France" in Ellerman & Morrison-Scott 1951:689).

Synonyms. [*Arvicola*] *12 costatus:* Selys, 1839 [variant spelling of *duodecimcostatus*]; *Arvicola Ibericus* Gerbe, 1854; *Pitymys ibericus centralis* Miller, 1908; *Pitymys ibericus regulus* Miller, 1908; *Pitymys ibericus fuscus* Miller, 1908 [preoccupied by *fuscus* Fatio, 1900 (=*Microtus subterraneus*)]; *Pitymys provincialis* Miller, 1909; *Pitymys ibericus pascuus* Miller, 1911 [new name for *Pitymys ibericus fuscus* Miller]; *Pitymys flavescens* Cabrera 1924.

Taxonomy. *M. duodecimcostatus* is a sister species to *lusitanicus*. Despite their molecular (Tougard 2017), chromosomal (Gornung et al. 2011b) and dental similarities (Miller 1912a), they differ cranially (Mathias 1996, Prieto 2013). Their ranges widely overlap in central and northern Spain (Extremadura, Castilla y Leon, La Rioja, Navarra, Basque country) and southern Portugal but the two species respond differently to soil conditions and vegetation (Santos et al. 2011) and dig in a species-specific manner (Winking 1976). Syntopic occurrence is rare in Portugal (Santos et al. 2009). Although there is evidence of historical *Mt*-DNA introgression from *duodecimcostatus* to *lusitanicus* (Bastos-Silveira et al. 2012), extensive karyotyping retrieved no interspecific F1 hybrids (Winking 1976). Crossbreeding experiments showed preferences for conspecific mates, reduced fertility in hybrid females and sterility in hybrid males (Winking 1976, Cerveira 2015).

Selys identified *duodecimcostatus* from "two skeletons, both presenting the anomaly of twelve (instead of thirteen) ribs" (Major 1905:508); Major discussed the appropriateness of Selys' name.

Distribution (Figure 281). Widespread and abundant across an area of 540,725 km² in southern France (Languedoc-Roussillon, Provence-Alpes-Cote d'Azur, and Rhône-Alpes; marginally in southern Aquitaine and southern Midi-Pyrenees), all of Spain (except Asturias and the majority of Galicia) and southern Portugal (Faro, Beja, Setubal, Évora, and southern Portalegre; very marginally present in Santarém, easternmost Bargança, Guarda, and Castelo Branco). Occupies open grassy habitats on deep and loose soil and prefers tall and dense vegetation cover; occasionally found in woods (Borghi et al. 1994, Santos et al. 2011). Elevational range is from sea level up to 2,170 m.

Characteristics. Dimensions: BWt=17–30 g, H&B=85–111 mm, TL=19–31 mm, HF=13–19 mm, EL=5.5–10 mm, CbL=21.7–26.9 mm, ZgW=13.5–17.1 mm, MxT=4.9–6.4 mm. Pine vole of modest size with a comparatively large and blunt head, characteristically small eyes, protruding incisors, reduced ears which are almost hidden in the fur, and a short tail (TL/H&B=0.20–0.30). Pelage is dense and mole-like and the protruding hairs (average length=10.2 mm) are only slightly longer than normal hairs (length=9.5 mm; Niethammer & Krapp 1982). General colour is usually pale, beige-grey to light wood-brown on the back and faintly sprinkled with black hair tips. Flanks usually show a cream-buff tint;

they are distinctly demarcated from the whitish or greyish belly. Feet are of similar colour as the belly and the tail is indistinctly bi-chromatic (light brownish above).

The skull is characterised by widely bowed zygomatic arches (ZgW/CbL=0.57–69) which spread abruptly; the braincase is squarish and rather deep. The dorsal profile is gently convex and the occipital is obliquely truncated hence the occipital condyles are readily seen when the skull is viewed from above. Temporal ridges are weak and only rarely approach each other; interorbital region is wide. Auditory bullae are well-developed and smooth (Figure 279). The mandible has a powerful articular process, a sickle shaped coronoid process, and a small angular process; the alveolar process forms a prominent bulge on the lateral wall when the mandibular ramus is viewed from behind (Figure 264a). Upper incisors are obviously proodont and their entire front face is visible when the skull is observed dorsally. The most peculiar of the molars is M^3 with a vestigial anterolateral triangle T2 which broadly communicates with T3 in >90% of cases. The posterior cap is usually simple and confluent with dental fields of T4–T5; T4 is isolated in ~15% of cases (Winking 1976). M_1 has the shortest posteroconid complex relative to the anteroconid complex in the subgenus (Brunet-Lecomte 1990). The trefoil is robust and the re-entrant angles LR5 and BR4 remain widely apart; noteworthy, in ~13% of cases, angles LR4 and BR3 are not deep enough to isolate the trefoil from the dental lamina formed by T4–T5 (Figure 280).

Karyotype: 2n=62, NF_a=72–78; difference in NF_a is due to changes in the position of the centromere in 4 autosomal pairs. The X chromosome is large bi-armed and the Y is small acrocentric (Winking 1976, Zima & Král 1984).

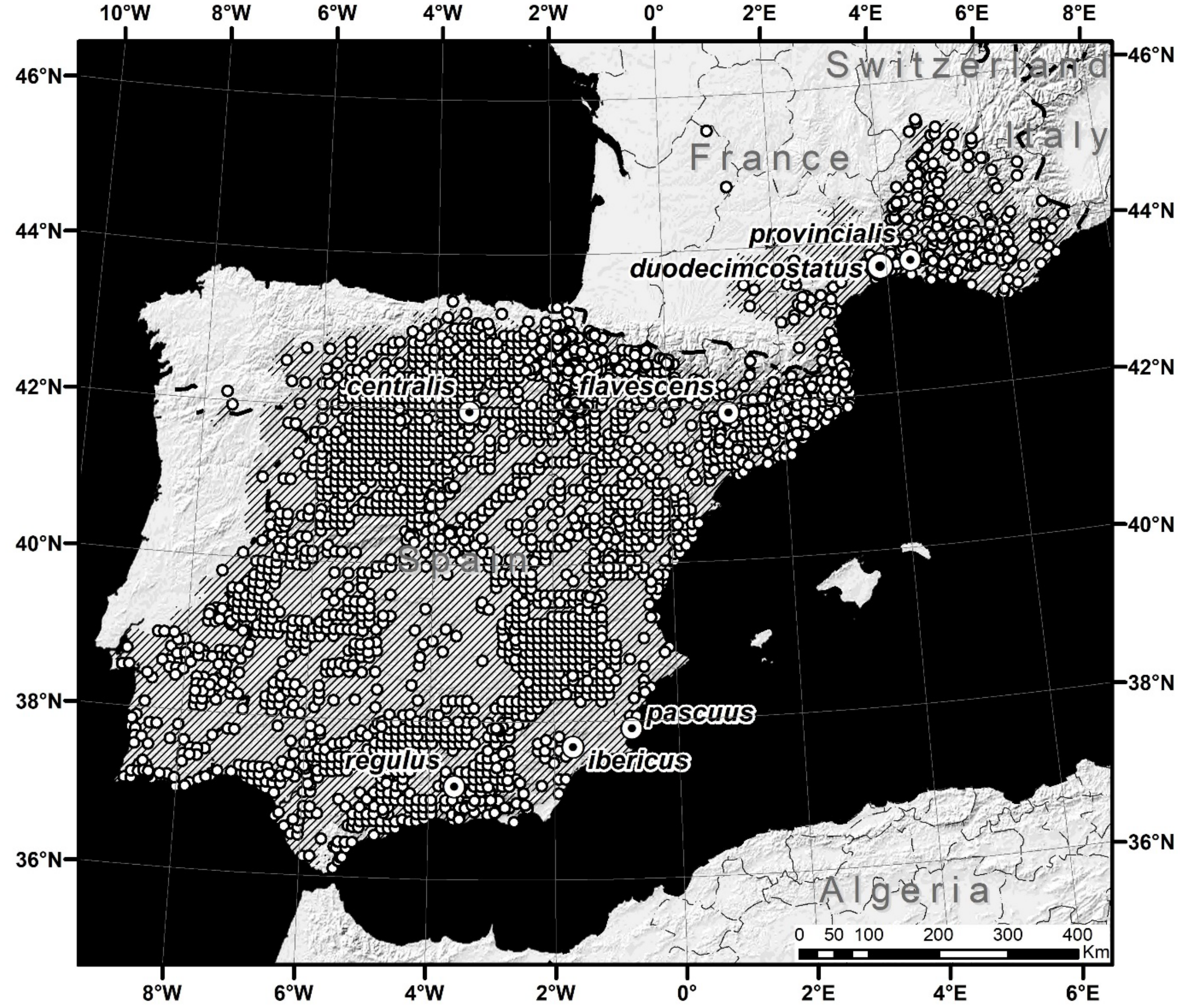


Figure 281: Distributional range of the Mediterranean pine vole *Microtus duodecimcostatus*.

Variation and subspecies. Interpopulation heterogeneity was reported in colour (Miller 1912a), size (Niethammer & Krapp 1982), degree of proodonty (Mathias 1990) and morphology of M_1 (Brunet-Lecomte 2004). Size varies clinally in the Iberian Peninsula (Palomo & Gisbert 2002) and the degree of proodonty correlates to the environment (Mathias *l.c.*). Genetically, the Mediterranean pine vole is composed of a single unstructured group of populations which share a p53 protein with a single mutation (Quina et al. 2015). Monotypic (Niethammer & Krapp 1982, Pardiñas et al. 2017).

Microtus lusitanicus Gerbe, 1879 – Lusitanian Pine Vole

Arvicola (Microtus) lusitanicus Gerbe, 1879b:44. Type locality is Portugal by tautonomy ("Campagnol du Portugal"). Major (1905:513) restricted type locality to "Cintra", where the type series was collected. Trouessart (1897:556) quotes an earlier albeit invalid naming of *lusitanicus* by Gerbe in 1854. We were unable to locate the paper.

Synonyms. *Microtus (Pitymys) mariæ* Major, 1905; *Pitymys depressus* Miller, 1908 [preoccupied by *depressa* Rörig & Börner, 1905 (=*M. arvalis*)]; *Pitymys pelandonius* Miller, 1908; *Pitymys mariae hurdanensis* Agacino, 1938; *Microtus (Pitymys) savii gerritmilleri* Kretzoi, 1958 [new name for *depressus* Miller].

Taxonomy. Long known as a subspecies of *savii* or under the name *mariae* (e.g. Heim & Beaufort 1967).

Distribution (Figure 282). Widespread and abundant across an area of 259,400 km^2 in north-central and north-western Spain (Galicia, Asturias, Cantabria, Castilla y Leon, Madrid, Basque Country, La Rioja, and Navarra; marginally in northern Extremadura and Aragon) and Portugal where they are sporadic in the south (Fara and Bejo); marginally present in the

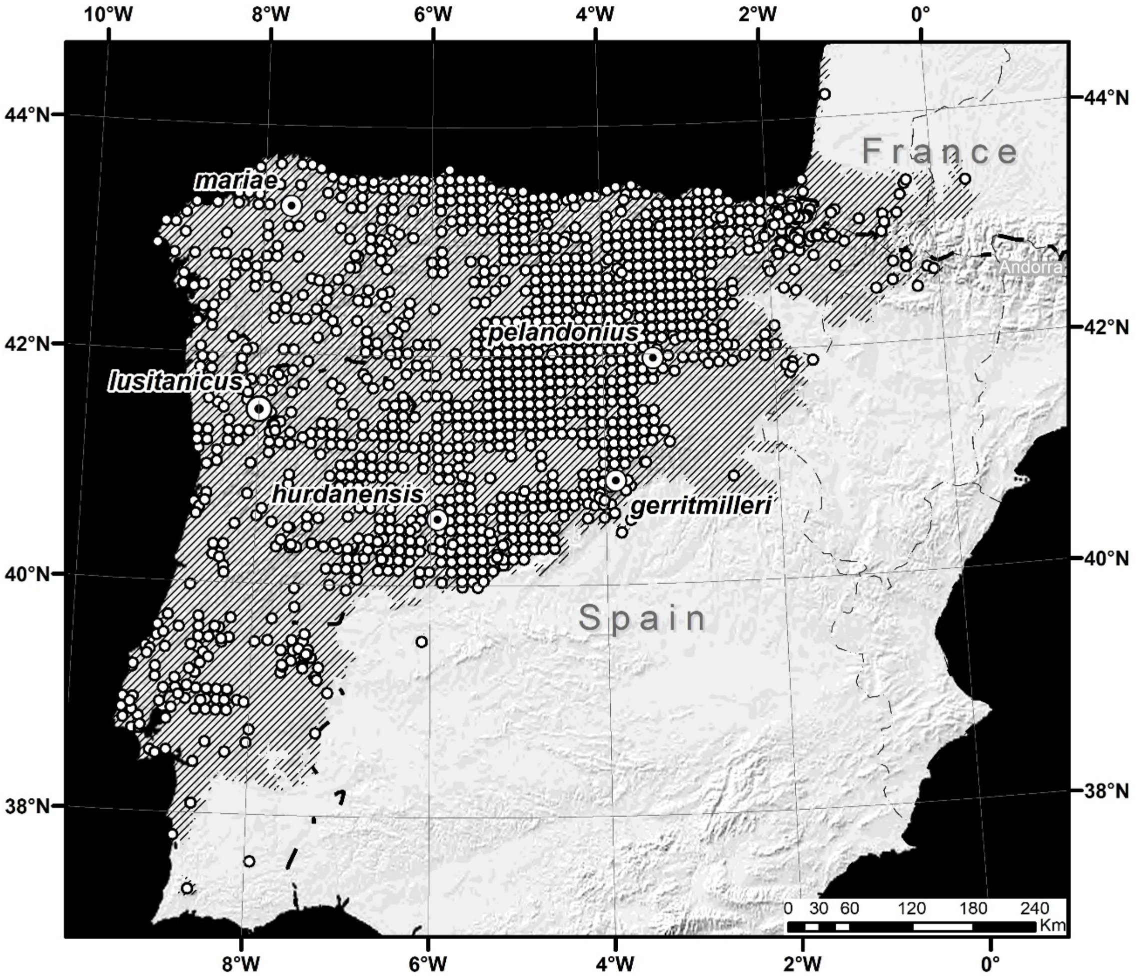


Figure 282: Distributional range of the Lusitanian pine vole *Microtus lusitanicus*.

western French Pyrenees (southern Aquitaine and south-western Midi-Pyrénées). The Lusitanian pine vole is an unspecialised opportunist living in a variety of habitat types (meadows, pastures, woods, agricultural areas). Less dependent on a deep soil layer than *duodecimcostatus* (Borghi et al. 1994) but seeks more humid sites (Santos et al. 2010). Elevational range is from sea level up to 2,035 m.

Characteristics. The smallest member of the *duodecimcostatus* group and one of the smallest pine voles: BWt=13.5–23 g, H&B=72–98 mm, TL=18–31 mm, HF=13–15.7 mm, EL=7–9 mm, CbL=18.9–23.6 mm, ZgW=12.1–15.0 mm, MxT=4.7–6.2 mm. The tail is longer than in *duodecimcostatus* (TL/H&B=0.23–0.38). Pelage is duller: dark brown dorsally and faintly grizzled by black and light hair tips; belly is grey and frequently shaded buffy. Flanks tend to be more buff than the back and are distinctly demarcated from the belly. Tail is obscurely bi-coloured, dusky above, buffy white below; feet are whitish to buffy grey. Skull is small, lightly built and shallower than in *duodecimcostatus*; the dorsal profile is gently bowed (Figure 279). The zygomatic arches are slightly less expanded (ZgW/CbL=0.57–0.68). The alveolar process on the lateral wall of the mandibular ramus is feeble (Figure 264b). The upper incisors vary from moderately proodont to nearly vertical; although *lusitanicus* is on average less proodont than *duodecimcostatus*, there is broad overlap between the two (cf. Mathias 1990). Molars are essentially as in *duodecimcostatus* but comparatively longer; average MxT/length of diastema=0.85 (0.77 in *duodecimcostatus*). The triangle T2 of M^3 broadly communicates with T3 in ~80% of cases; the lamina formed by the dental fields of these triangles is isolated from T4 and the posterior cap (Winking 1976). M_1 is very similar to *duodecimcostatus* except for having a slightly longer posteroconid complex relative to the anteroconid complex (Brunet-Lecomte 1990); re-entrant angles LR4 and BR3 are on average deeper and the trefoil connects with the dental lamina of T4–T5 in ~4% of cases (Figure 280).

Karyotype: 2n=62, NF_a=70–74; there are 5–6 bi-armed and 24–25 acrocentric autosomes; sex chromosomes are either acrocentric or bi-armed (Winking & Niethammer 1970, Winking 1976).

Variation and subspecies. Variation between populations was reported in cranial shape (Miller 1912a), degree of proodonty (Mathias 1990), enamel molar pattern (Winking 1976, Brunet-Lecomte 1990) and karyotype (Winking 1976). Voles from central Portugal are characterised by wider zygomatic arches and a deeper braincase (Winking 1976). Winking (*l.c.*) found significant interpopulation variation in the interorbital width (a north-to-south increase) but not in the skull length. The centromeric position of the autosomal pair 2 and the Y chromosome vary geographically. The Y chromosome is acrocentric north of Calda de Rainha–Bilbao and bi-armed to its south. The autosome 2 is normally metacentric except in central Portugal and Puerto de Somosierra (the Central System, Spain) where it is submetacentric (Winking 1976). Subspecific taxonomy is controversial. Some authors (Pardiñas et al. 2017) accepted 2 subspecies, the nominal (with *gerritmilleri* and *hurdanensis*) in the south and *mariae* (with *pelandonius*) in the north. Groupings based on different datasets are not congruent; doubts have been expressed as to whether subspecies can be objectively delimited (e.g. Madureira & Ramalhinho 1982.)

Microtus pyrenaicus (Sélys, 1847) – Pyrenean Pine Vole

A[*rvicola*] *pyrenaicus* Sélys, 1847:305. Type locality: "The Pyrenees, at high elevation, in the cold regions of Pic du Midi [de Biggore]", France. Not "Bagnères de Bigorre, Hautes-Pyrénées" (Miller 1912a:771) which is usually quoted as the type locality. Bagnères de Bigorre is a town in the foothills of the Pyrenees (the type is from "high elevation") and an administrative division (arrondisement), which only partly encompasses Pic du Midi de Biggore (Brunet-Lecomte 2010).

Synonyms. *Arvicola (Microtus) gerbii Lisle, 1879* [*in Gerbe 1879*]*; Pitymys pyrenaicus brunneus* Miller, 1908; *Pitymys planiceps* Miller, 1908.

Taxonomy and nomenclature. The name *pyrenaicus* has a complicated taxonomic and nomenclatural history and French authors started using it in its current sense as late as the 1970s (Saint Girons 1973, Louarn & Saint Girons 1977). Since then, Musser & Carleton (1993:521) replaced *pyrenaicus*, an established name (e.g. Niethammer & Krapp 1982), with "*Microtus gerbei* (Gerbe, 1879)". This was based on Spitz (1978:286) who questioned the taxonomic identity of *pyrenaicus* as defined by Miller (1912a) without studying Miller's vouchers. Instead, Spitz built his argument against Miller on samples from Arreau and Aulus-les-Bains which he thought were *lusitanicus* although both localities are outside its range. We therefore reject the interpretation made by Spitz and reinstall *pyrenaicus* as a valid name for the Pyrenean pine vole; *pyrenaicus* involves no ambiguity since neither *lusitanicus* nor *duodecimcostatus* have been documented within a 40–50 km radius of its type locality (cf. Figures 281–283).

Distribution (Figure 283). France to the south and west of the Loire River and the Pyrenees. The entire range covers an estimated 172,650 km² covering north-eastern Spain (Catalonia, Aragon, Navarra, and Basque Country, La Rioja, eastern Cantabria, and north-eastern Castilla y Leon) and France (Aquitaine, Midi-Pyrénées, Poitou-Charentes, Limousin, and western Auvergne, reaching south-western Pays de la Loire). These are generalist voles occurring wherever the soil is deep enough for burrowing and covered by dense vegetation to provide shelter (Borghi et al. 1994). Common in forest clearings and along

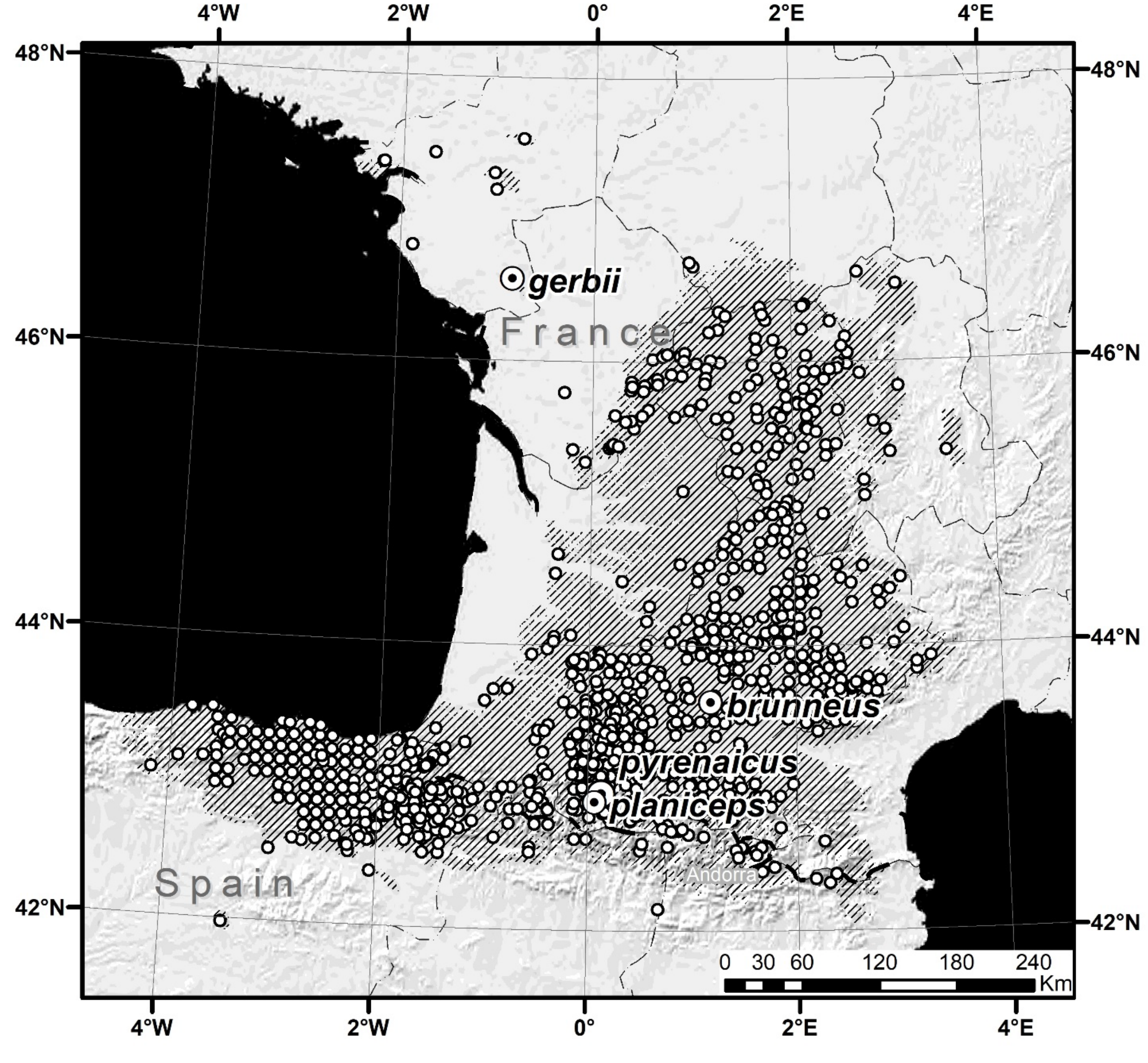


Figure 283: Distributional range of the Pyrenean pine vole *Microtus pyrenaicus*.

watercourses. Elevational range is from sea level up to 1,970 m.

Characteristics. A large member of the group: BWt=17–23 g, H&B=92–108 mm, TL=26–37 mm, HF=14.5–17.4 mm, EL=7–9 mm, CbL=22.0–26.3 mm, ZgW=13.0–16.9 mm, MxT=4.9–6.6 mm. The tail is longer (TL/H&B=0.27–0.36) than in *duodecimcostatus*; the external appearance and colour are as in *lusitanicus*. The baculum is of a standard trident type with a comparatively small trident (length of medial digit=0.8 mm). The proximal baculum (length=2.5 mm) has an expanded basal spatula (Didier 1954). The skull is large and heavy (Figure 279); its most prominent feature are slender nasals (width/length of nasal=0.37–0.42, vs 0.42–0.49 in *duodecimcostatus* and 0.44–0.51 in *lusitanicus*). The alveolar process forms a prominent bulge on the lateral wall of the mandibular ramus. Upper incisors are slightly proodont or vertical; the anterior outer triangle T2 is on average larger and frequently isolated (Figure 280). Karyotype: $2n=54$, $NF_a=56$; both sex chromosomes are acrocentric and the X is the largest chromosome in the set (Winking & Niethammer 1970, Meylan 1974).

Variation and subspecies. No subspecies are recognised (Saint Girons 1973, Niethammer & Krapp 1982).

Species group *multiplex*

Taxonomy. Morphologically heterogeneous group which is reasonably well-supported in molecular reconstructions. The 5 species as recognised here stem from the terminal branching of pine voles (Tougard 2017). In the past, these voles were usually dispersed among all the major supraspecies assemblies (see under species).

Distribution. Mountains and foothills in Central Europe (the Alps and Carpathians) and south-eastern Europe (western Balkans).

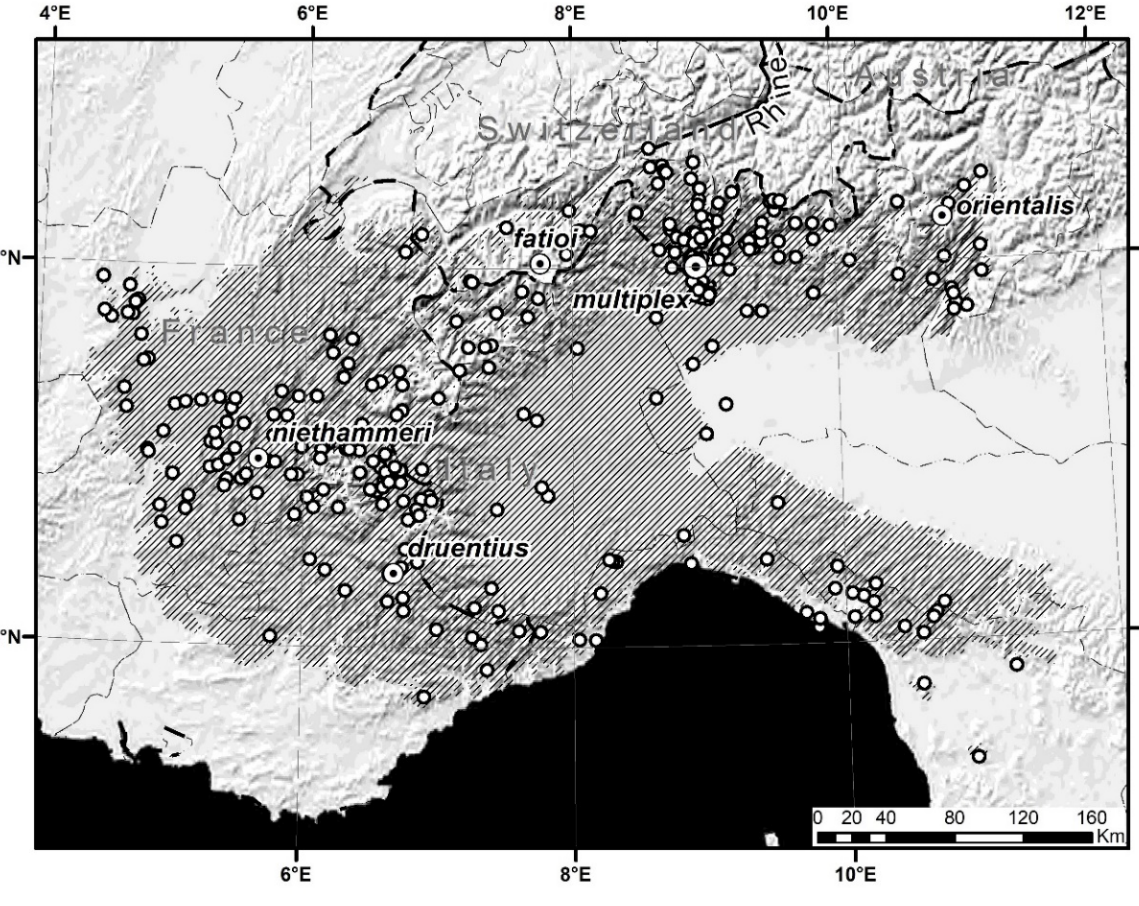


Figure 284: Distributional range of the Alpine pine vole *Microtus multiplex*.

Microtus multiplex (Fatio, 1905) – Alpine Pine Vole

[Arvicola] multiplex Fatio, 1905:193. Syntypes are from the "Bassin of Léman [Lake Geneva], […] at about 1800 m above sea level in the Alpes Vaudoises [and] … Vidy near Lausanne", south-western Switzerland.

Synonyms. *Arvicola (Microtus) selysii* Gerbe, 1852 [antedated by *selysii* Bonaparte, 1845 (=*M. savii*)]; *M[icrotus] leponticus* Thomas, 1906 [unavailable name]; *P[itymys] multiplex fatioi* Mottaz, 1909; *Pitymys druentius* Miller, 1911 [new name for *selysii* Gerbe, 1852]; *Pitymys fatioi orientalis* Dal Piaz, 1924; *Microtus (Terricola) multiplex niethammeri* Brunet-Lecomte & Volobouev, 1994.

Taxonomy. Ellerman & Morrison-Scott (1951) synonymised *multiplex,* like all pine voles with a complex M^3 with *subterraneus.* Such a taxonomic status however was short-lived since chromosomal evidence, which became available around the same time, exposed a profound difference between these taxa *(*Matthey 1955). Subsequent studies revealed lowered reproductive output in *multiplex*×*subterraneus* pairing with sterile hybrid males; hybrids were never found in nature (Meylan 1972, 1974).

One among synonyms of *multiplex* was *liechtensteini* (Đulić & Mirić 1967) which was described as an independent species from north-western Croatia (Wettstein 1927). It was subsequently shown (Storch & Winking 1977) that these taxa differ karyologically (2n=48 in *multiplex* and 46 in *liechtensteini*) and occupy exclusive ranges, however a single F1 hybrid was retrieved from the parapatric zone in the upper Adige valley (South Tyrol, Italian Alps). Opinions differed for decades as to the taxonomic status of these chromosomal forms; based on *Mt*-distance (e.g Jaarola et al. 2004) we rank them as a distinct species.

Distribution (Figure 284). Western Alps in south-eastern France (Provence-Alpes-Côte d'Azur and Rhône-Alpes), southern Switzerland (Graubünden, Ticino, Uri, and Valais), and north-western Italy. Range in Italy is on the edge of the Alps (between Valle d'Aosta and Trentino Alto Adige), along the Ligurian coast and in the Ligurian Alps (marginally includes Tuscany), as well as in the watershed of the upper Po River in Lombardy and Piedmont. *M. multiplex* is a dweller of deep humid soils with dense vegetation, from low-lying meadows to sparse mountain forests. Altitudinal span is from sea level up to 2,300 m. The entire range is estimated at 99,030 km². Sympatric with *subterraneus* and *savii.*

Characteristics. A large pine vole with a rather short tail (TL/H&B=0.26–0.43). Dimensions: BWt=19–30 g, H&B=91–111 mm, TL=27–33 mm, HF=14–17 mm, EL=8–10 mm, CbL=22.8–26.6 mm, ZgW=12.9–15.6 mm, MxT=5.2–6.8 mm. Ears are shorter than in *subterraneus*, but data recorded by various collectors may confuse the matter due to inconsistencies scoring external measurements. Hind foot is more robust and the 5 plantar pads are on average smaller; females have 2 pairs of inguinal nipples. Fur is soft, dense and mole-like; hairs are 7.5–9 mm long and the plentiful protruding hairs are longer by 1.5 mm. The annulation on the tail is exposed and the terminal tuft of hair is modest (length=3 mm). Dorsal fur is deep brown, finely grizzled grey and black; the sides are usually more clear brown with a slight ochraceous shade. The belly is light grey, clouded with slate hair bases and in some animals shaded buff. Feet are thinly clothed with silvery greyish or white hairs, therefore contrasting the back; tail is obscurely bi-coloured, brown above, whitish below. Compared to *subterraneus*, the skull is on average slightly deeper with a more bowed dorsal profile and incisive foramina are proportionally longer (Figure 285). Molars also closely resemble the pattern seen in *subterraneus* (Figure 286a). Karyotype: 2n=48, NF_a=50; the X chromosome is medium-sized bi-armed, and the Y is small acrocentric. As a result of pericentric inversions, each located in a different region, the karyotype is polymorphic. Cytotypes are interfertile (Graf & Meylan 1980).

Variation and subspecies. On the basis of size differences, Miller (1912a) distinguished 3 monotypic species (*multiplex, druentius, fatioi*) which are occasionally classified as subspecies of *multiplex* (e.g. Amori et al. 2008). The majority of authors, however, hesitate to recognise a subspecies within *multiplex* s.str. (Niethammer & Krapp 1982, Shenbrot & Krasnov).

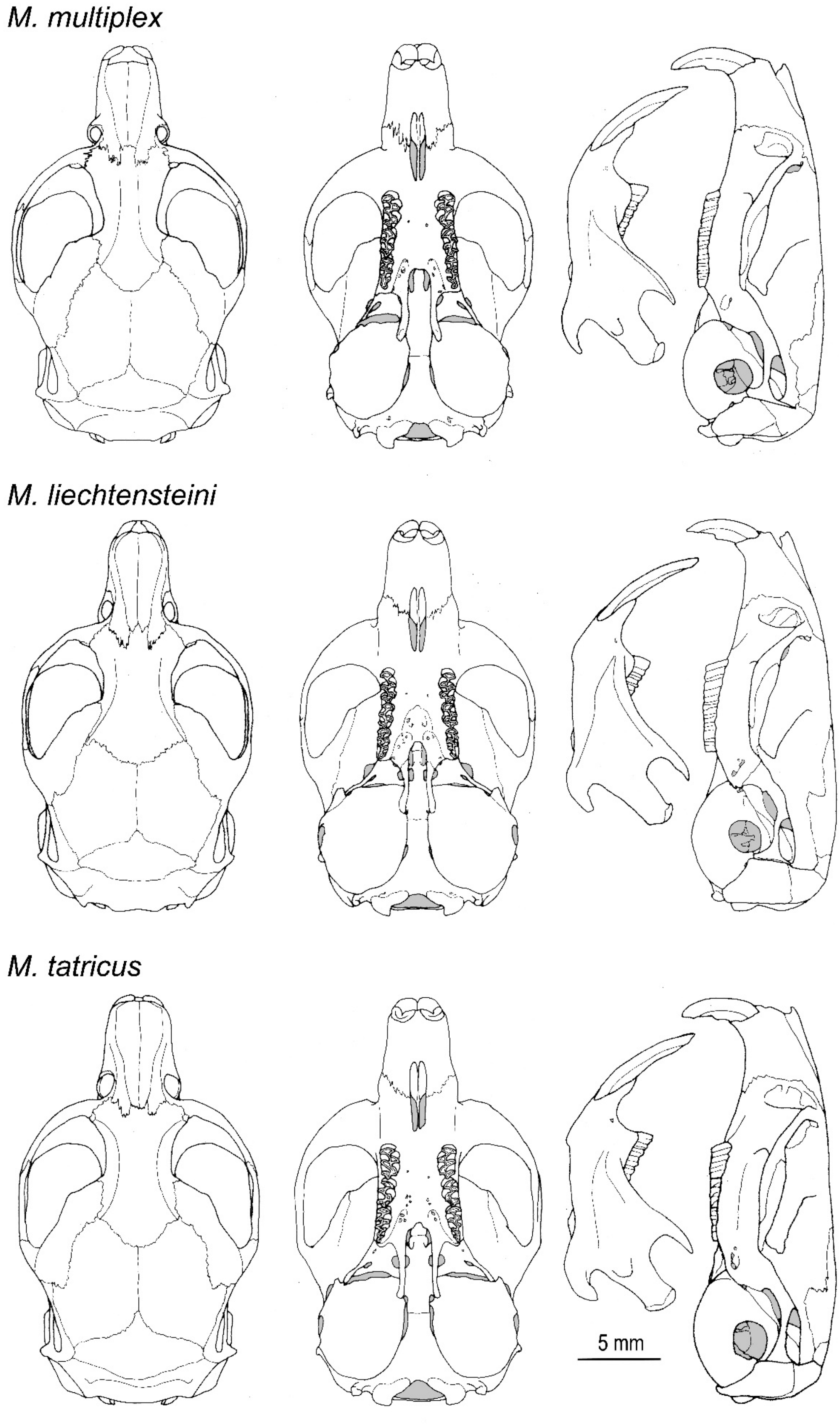


Figure 285: Skull in three pine voles of the *multiplex* species group: top–*Microtus multiplex* (Trentino, Italy); middle–*M. liechtensteini* (Mt. Snežnik, Slovenia); bottom–*M. tatricus* (High Tatra Mt., Slovakia).

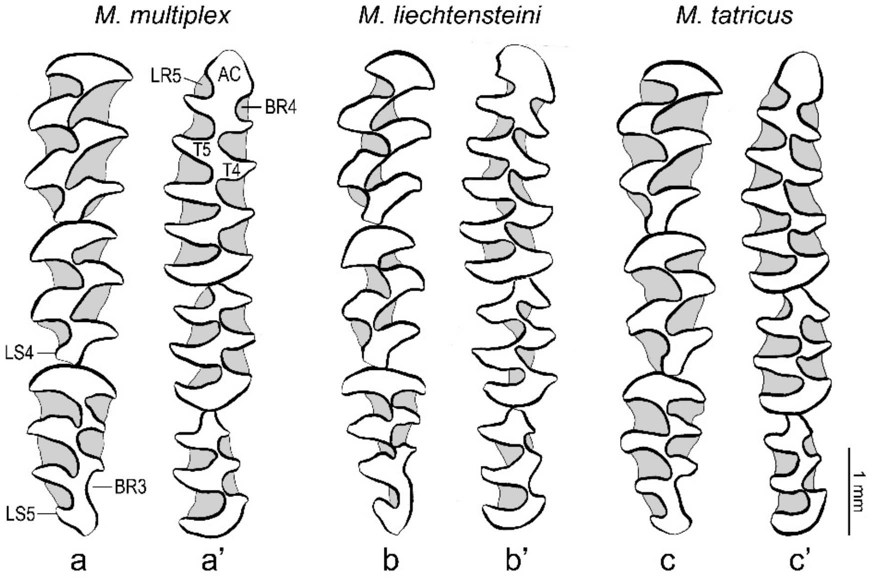


Figure 286: Molar pattern in pine voles of the *multiplex* species group. *Microtus multiplex*: upper (a) and lower row (a'–Trentino, Italy). *Microtus liechtensteini*: upper (d) and lower row (d'–Garmisch-Partenkirchen, Bavarian Alps, Germany). *Microtus tatricus*: upper (d) and lower row (d'–Vel'kà Fatra Mts., Slovakia).

Microtus liechtensteini (Wettstein, 1927) – Liechtenstein's Pine Vole

Pitymys liechtensteini Wettstein, 1927:2. Type locality: "Peak of Mali Rainac, 1699 m, northern Velebit [Mts.] near Krasno, Croatia."

Synonyms. *Pitymys bavaricus* König, 1962; *Pitymys liechtensteini petrovi* Kryštufek, 1983.

Taxonomy. A sister species to *multiplex*. Molecular phylogenetics showed that *M. bavaricus*, an enigmatic taxon which was known only from its type locality in southern Bavaria for a considerable period of time, is

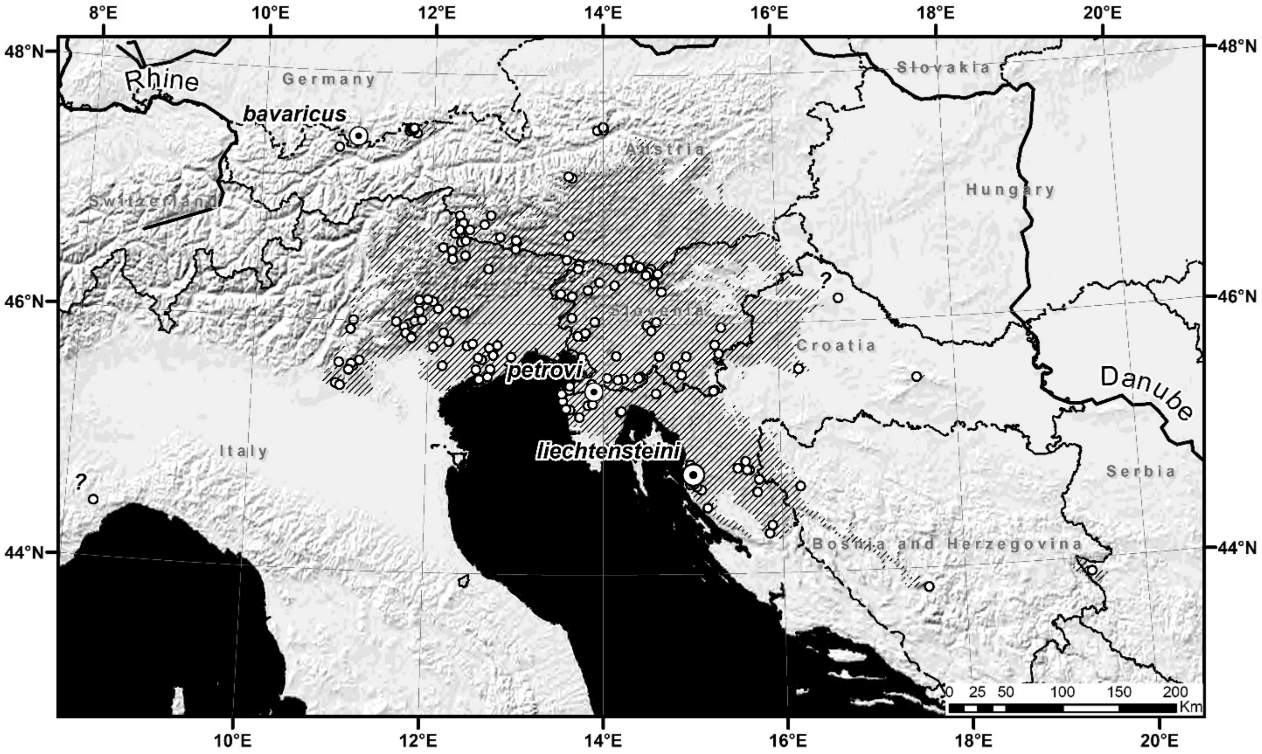


Figure 287: Distributional range of Liechtenstein's pine vole *Microtus liechtensteini*.

close to *lichtensteini* (Haring et al. 2000). These 2 voles share an identical karyotype and show the level of genetic differentiation which is of intraspecific value (Martínková et al. 2007); *bavaricus* haplotypes are scattered far apart in Bavaria, Tyrol (Austria) and northern Croatia (Tvrtković et al. 2010) therefore suggesting that a phenomenon of ancient polymorphism is in question in *liechtensteini*, rather than a cryptic species (Meinig et al. 2020).

Distribution (Figure 287). The range encompasses mountainous areas and plains around the Northern Adriatic and stretches contiguously from the Eastern Alps in Italy (Friuli-Venezia Giulia, Trentino Alto Adige, and Veneto), south-eastern Tyrol, Carinthia (Austria), and north-western Slovenia. From the Alps the range extends across the adjacent Padan Plain (Italy) towards the Adriatic Sea and encompasses northern Istria and the Dinaric Alps in south-western Slovenia and north-western Croatia as far south as Mt. Velebit extends. Isolated records are scattered all around the periphery in Liguria (Italy; Haring et al. 2000), southern Bavaria (Germany; Kraft 2008), adjacent northern Tyrol and western Styria in Austria (Martínková et al. 2007), northern Croatia (Tvrtković et al. 1979, 2010), central Bosnia (Kryštufek 1984) and western Serbia (Živković et al. 1975); some of these records require verification. Distribution area is estimated at 68,830 km^2. Habitat requirements are as in *multiplex*, and the elevational range is from sea level up to 1,875 m. This vole is sympatric with *subterraneus* and *savii*.

Characteristics (Figure 262c). Dimensions: BWt=18–32.5 g, H&B=86–114 mm, TL=27–41 mm, HF=14.2–17.1 mm, EL=5.7–10.2 mm, CbL=22.1–25.8 mm, ZgW=13.3–15.5 mm, MxT=5.4–6.6 mm. Morphologically not distinguishable from *multiplex*; size is slightly smaller, the tail is proportionally shorter (TL/H&B=0.27–0.39), and bullae are on average smaller (=5.93–7.29 mm *vs* 6.23–8.66 mm in *multiplex*; Amori et al. 2008). Karyotype: 2n=46, NF$_a$=48; X chromosome is bi-armed and Y chromosome is either subtelocentric or metacentric (Živković et al. 1975, Zima & Král 1984).

Variation and subspecies. Meinig et al. (2020) classify *bavaricus* as a valid subspecies, however without specifying its range and diagnostic traits. Liechtenstein's pine voles from Istria (described as *petrovi*) are on average larger, show a high proportion of anomalies on M^1, and have a more open anterior loop on M$_1$ (Brunet-Lecomte & Kryštufek 1993).

Microtus tatricus (Kratochvíl, 1952) – Carpathian Pine Vole

Taxonomy. Since its discovery in the early 1950s, *tatricus* was nearly uniformly accepted as a species in its own right and classified either in the *subterraneus* group (Chaline et al. 1988) or *multiplex* group (Zagorodnyuk 1989, Chaline et al. 1999). The close relationship of *tatricus, multiplex* and *liechtensteini*, as postulated from morphological evidence, is also supported by molecular analyses (Haring et al. 2000, Martinková & Moravec 2012). *Microtus tatricus* and *multiplex* produced fertile hybrids under captive conditions (Gromov & Erbajeva 1995).

Distribution (Figure 288). The Carpathian mountain range in Slovakia (Tatra Mts., Oravské Beskydy, Vel'ká and Malá Fatra, Muranska Planina), Poland (Oravské Beskydy), Ukraine (Eastern Carpathians), and Romania (Rodnei, Ciucas, Calimani, and Muramareş Mts.). The range is small (9,225 km^2) and fragmented at various scales. The most obvious is a gap between the western fragment in Slovakia and Poland and the eastern fragment in Ukraine and northern Romania. The population in the Ciucas Mts. is a far southern isolate. Altitudinal range is 600–2,343 m and the majority of records are at 1,100–1,700 m. *M. tatricus* prefers open habitats with high humidity, dense herbage layer and rocks in the zone of broadleaf and spruce forests and in the subalpine belt (Zagorodnyuk et al. 1992, Martinková & Dudich 2003). Sympatric with *subterraneus*.

Characteristics (Figure 262e). A large and long-tailed (TL/H&B=0.35–0.41) pine vole. Its appearance is similar to *agrestis* or *arvalis* which results in frequent misidentifications in the field (Zagorodnyuk et al.

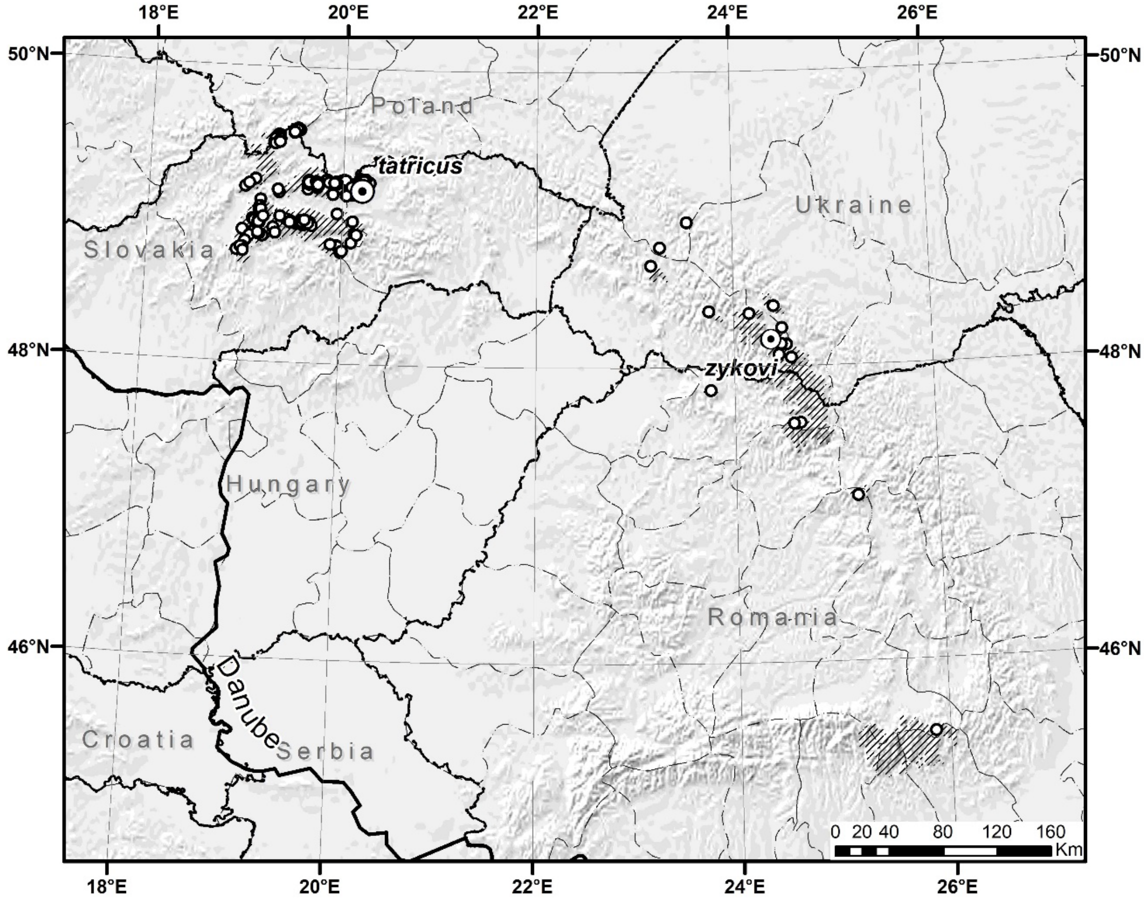


Figure 288: Distributional range of the Carpathian pine vole *Microtus tatricus*.

1992). The ears are comparatively long and the eyes are larger (diameter=2.1–2.3 mm; Kratochvíl 1964) than in *subterraneus* or *multiplex*. Fur is long and coarser than in sympatric *subterraneus*; back is dull ochraceous-buff, belly is silver to grey, lightly shaded buff, demarcation along flanks is fairly obvious. The tail is bi-coloured, dark brown above, cream below; the terminal pencil is prominent. Feet are whitish and have 6 plantar pads; the lateral metatarsal pad is tiny (Figure 263c). Females have 2 inguinal pairs of nipples. Baculum is of characteristic trident shape; the proximal bone is 2.6–2.8 mm long and 1.2–1.4 mm wide; the central and the lateral distal digits measure 1.0–2.2 mm and 0.8–0.9 mm, respectively (Hrabě 1972). Skull is large but otherwise shows no peculiarities; on average deeper than in *subterraneus*; the dorsal profile is straight or slightly concave (Figure 285). The interorbital region is wide and supratemporal ridges are obvious. Molar pattern is essentially as in *multiplex*; M_1 normally has 5 inner and 4 outer re-entrant angles. M^3 is with 4 lingual salient angles and 3–4 labial salients; ~8.5% of individuals from Slovakia display a simple M^3 morphotype, having only 2 inner salient angles (Kratochvíl 1970). M^2 rarely has an additional postero-lingual salient angle (LS4c).

Karyotype possesses highly derived features, i.e. a low diploid number (2n=32) and unique combinations of arms in 7 pairs of bi-armed autosomal chromosomes (NF_a=44); both heterosomes are bi-armed (Matthey 1964, Zagorodnyuk & Zima 1992).

Variation and subspecies. Two subspecies are usually recognised (Gromov & Erbajeva 1995, Shenbrot & Krasnov 2005, Pardiñas et al. 2017). They differ in size while the karyotype displays no differences between them (Zagorodnyuk & Zima 1992).

Microtus tatricus tatricus (Kratochvíl, 1952)

Pitymys tatricus Kratochvíl, 1952:174. Type locality by subsequent designation (Kratochvíl 1970:5): "Velkà

Studenà dolina [Valley] above Kamzík-Baude in a montane forest *Sorbeto-Piceetum* […] at the altitude of about 1600 m", High Tatra Mts., Slovakia.

Distribution. Poland and Slovakia.

Characteristics. Larger: BWt=25.5–36 g, H&B=96–116 mm, TL=37–49 mm, HF=16.5–18 mm, EL=9–13 mm, CbL=23.9–26.0 mm, ZgW=14.0–15.3 mm, MxT=5.9–6.4 mm. Skull is deeper: height of rostrum=6.1–6.8 mm (vs 5.4–6.4 mm in *zykovi*); height of braincase across bullae=8.4–9.2 mm (vs 8.2–8.6 mm in *zykovi*; Zagorodnyuk 1989).

Microtus tatricus zykovi (Zagorodnyuk, 1989)

Terricola tatricus zykovi Zagorodnyuk, 1989:7. Type locality: "Zakarpatskaya Obl[ast], Rachovskiy ('Tyachevskiy') Rayon, R. Goverlyanka, western slope of Mt. Petroe (800–1200 m)", Ukraine.

Distribution. Romania and Ukraine.

Characteristics. Smaller: BWt=27.2–29.5 g, H&B=93–110 mm, TL=36–41 mm, HF=16–17 mm, EL=8–11 mm, CbL=23.4–25.0 mm, ZgW=13.7–14.3 mm, MxT=5.9–6.4 mm (Zagorodnyuk et al. 1992). Skull is shallower (see above).

Microtus thomasi (Barrett-Hamilton, 1903) – Thomas' Pine Vole

Microtus (Pitymys) Thomasi Barrett-Hamilton, 1903:306. Type locality: "Vranici [Vranići near Podgorica], Montenegro".

Synonyms. *Pitymys atticus* Miller, 1910; *Pitymys Byroni* Bolkay, 1926; *M[icrotus] (T[erricola]) t[homasi] evia* Tougard, 2017:49 (Table 1) [nomen nudum].

Taxonomy. Thomas' pine vole was described under two names, *thomasi* and *atticus,* which were subsequently synonymised with *M. duodecimcostatus* (Ellerman & Morrison-Scott 1951) and again reinstalled as two species, *atticus* (Kratochvíl 1971) and *thomasi* (Petrov & Živković 1979). Niethammer (1974) considered them to be conspecific and since the 1970s Thomas' pine vole has been nearly uniformly known as *thomasi*. Rovatsos & Giagia-Athanasopoulou (2012) reported on the near total reproductive isolation between *thomasi* and *atticus* and argued for their reinstalment as distinct species. If their proposal is accepted, a low genetic divergence between these two taxa will likely necessitate a further taxonomic split in pine voles in order to avoid disparity in the criteria applied to the species delimitation. We therefore continue to rank *thomasi* and *atticus* as two well-differentiated lineages.

Molecular evidence placed *M. thomasi* as a sister to *M. felteni* (Martínková & Moravec 2012; but see Thanou et al. 2012, for a different conclusion). In the past, *thomasi* was in the *ibericus* species group with *duodecimcostatus* and *lusitanicus* (Miller 1912a). Zagorodnyuk (1990) classified *thomasi*, together with *savii, pyrenaicus* and *duodecimcostatus,* in the subgenus *Meridiopitymys*. Based on the M^3 morphology, specifically the large size and supposedly archaic shape of the anterior part of the tooth, Brunet-Lecomte & Nadachowski (1994:157) concluded that *M. thomasi* "should be distinguished as a separate species group of the subgenus *Terricola*".

Distribution (Figure 291). Endemic to the western Balkan Peninsula in south-eastern Bosnia and Herzegovina, Montenegro, Albania, and Greece as far east as the Axios River, and as far south as the Peloponnesus; also present on the Island of Euboea (Evia). The distributional area is estimated at 93,525 km². Altitudinal range is from sea level up to 950 m in the north and up to 1,985 m in Greece. Occupies grasslands, Mediterranean habitat mosaic, and light woodland.

Characteristics (Figure 262d). Large and robust vole with a blunt head and short tail (TL/H&B=0.16–0.23). Dimensions: BWt=18–43.5 g, H&B=89–119 mm, TL=12–30 mm, HF=14–18 mm, EL=7–11 mm, CbL=22.0–27.3 mm, ZgW=13.2–17.0 mm, MxT=5.4–6.9 mm. Fur is short (length=7–8.5 mm) and the sparse hairs protrude only by 1–1.5 mm; the tail is densely clad by hairs and the annulation is concealed; terminal pencil is prominent (length=3.5 mm). Dorsum is light to deep

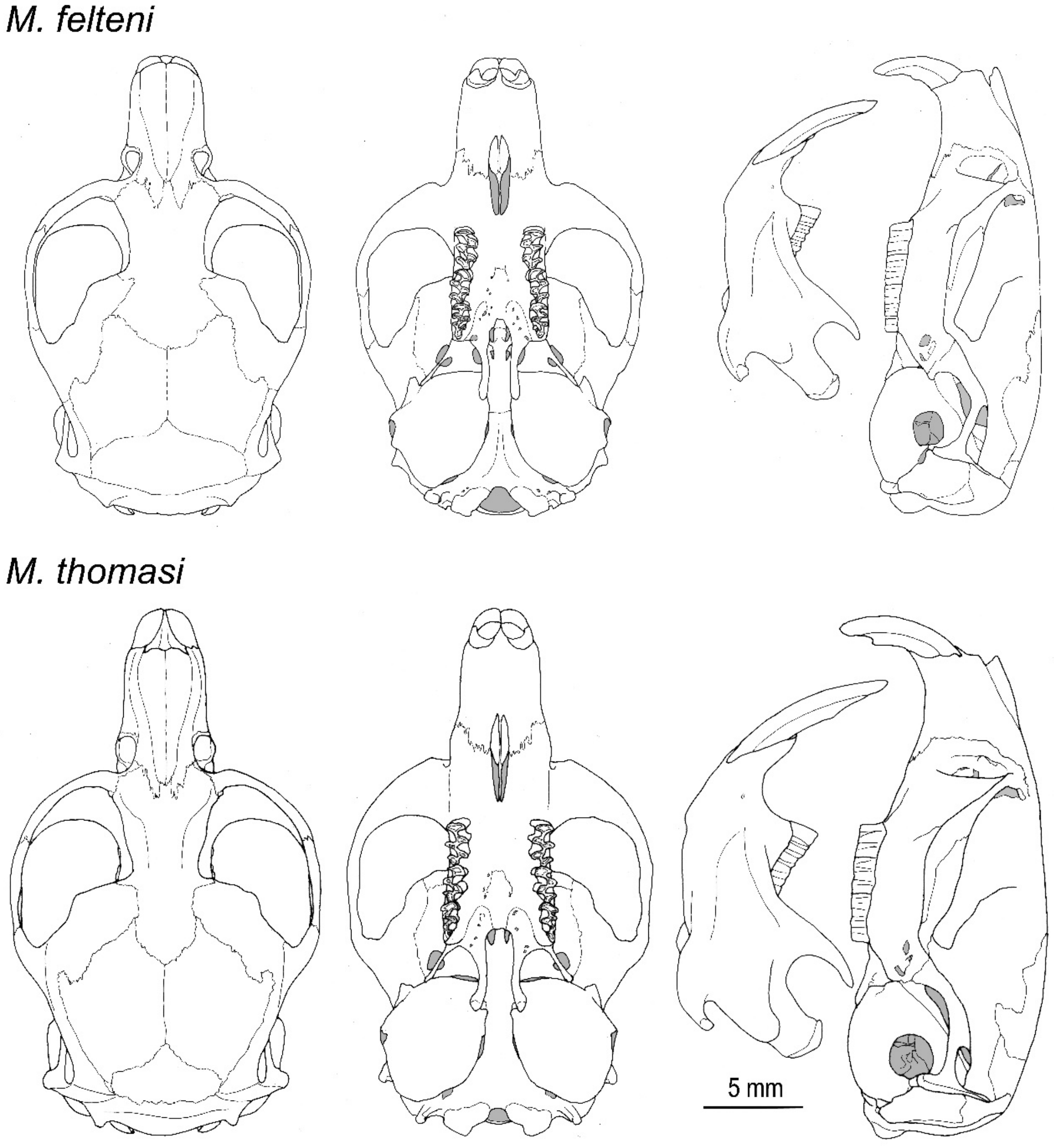


Figure 289: Skull in two pine voles of the *multiplex* species group: top–*Microtus felteni* (Mt. Baba, North Macedonia); bottom–*M. thomasi* (Trebinje, Bosnia and Herzegovina; bottom).

reddish brown, darker on the head and more buff on the flanks. Belly is grey to slate and washed buff; the transition along the flanks is rather abrupt. Tail is light buffy, obscurely bi-coloured, paws are whitish. There are 5 plantar pads Figure 263e); females have 3 pairs of nipples (1 pectoral and 2 inguinal pairs). Proximal baculum is 2.00–2.65 mm long and 1.00–1.42 mm wide across the base; the posterior margin is notched (Figure 265d). Central distal baculum is 0.63–0.93 mm long; lateral digits are small circular or remain cartilaginous. The skull is robust and deep with a slightly convex profile (Figure 289). Zygomatic arches spread abruptly (ZgW/CbL=0.58–0.64); braincase is relatively short, occiput is obliquely truncated, interorbital constriction is wide; bullae inflated. The mandible is low with a robust articular process and protuberant angular process. The incisors are proodont but less than in *M. duodecimcostatus* (Ondrias 1966, Niethammer 1974). The M^3 shows 2 deep re-entrant angles on each side and a short and wide posterior cap; the postero-lingual re-entrant angle LR4 is present in <20% of individuals. Dental fields T2–T3 are confluent in ~⅓ of cases and alternate in the rest; T4 opens into the posterior cap in ~⅔ of molars. M_1 is decidedly longer (mean =3.08 mm;

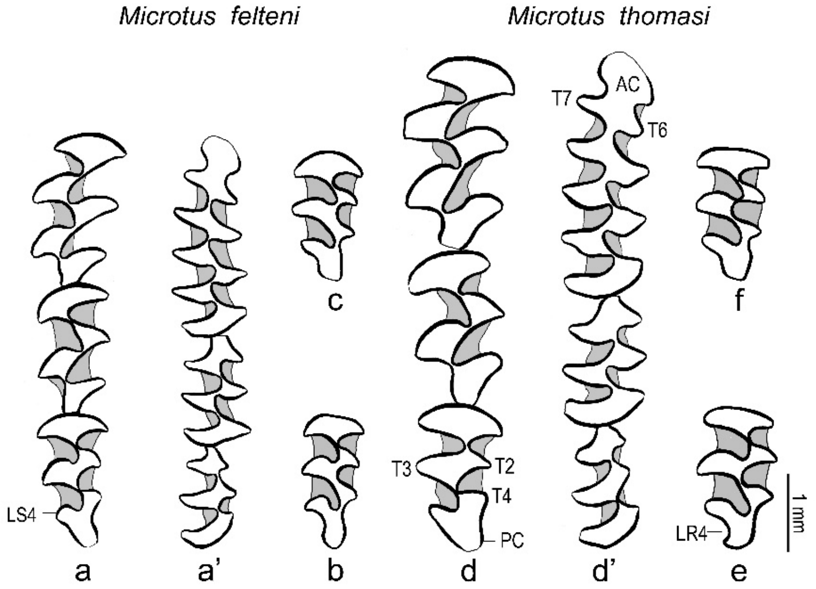


Figure 290: Molar pattern in two pine voles of the *multiplex* species group. *Microtus felteni*: upper (a) and lower row (a'–Popova Šapka, Šar planina Mts., North Macedonia); isolated M³ (b,c–Pertouli, Pindus Mts., Greece). *M. thomasi*: upper (d) and lower row (d'–Grahovo, Montenegro); isolated M³ (e–Githsou, Peloponnes, Greece; f–Agios Stefanos near Athens, Greece).

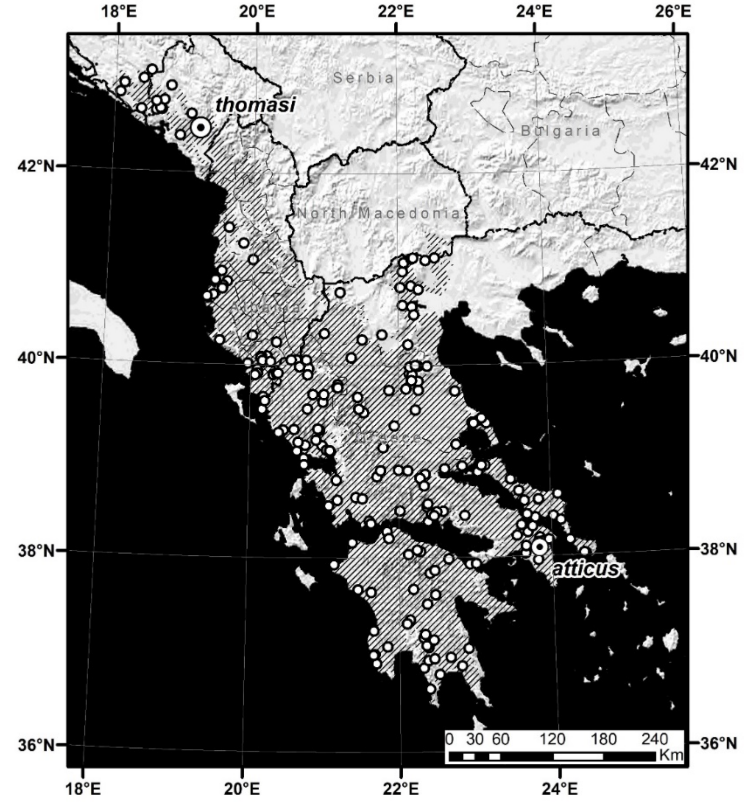


Figure 291: Distributional range of Thomas' pine vole *Microtus thomasi*.

Brunet-Lecomte & Nadachowski 1994) than in the remaining pine voles. Its anterior cap is always broadly confluent with triangles T6–T7. The anteroconid and the trigonid-talonid are of approximately the same length (Figure 290d-f).

M. thomasi shows high chromosomal variability with at least 7 chromosomal races having 2n=38, 40, 42, and 44, and NF_a=38, 40, and 42. The X chromosome is in 14 different acrocentric or subtelocentric variants which differ in size or arm length ratio due to a heterochromatin addition. The Y chromosome is known in 12 mainly acrocentric variants (Acosta et al. 2009, Rovatsos et al. 2021). Overall, the size of sex chromosomes increases from south to north (Mitsainas et al. 2009). The all-acrocentric northern cytotype 2n=NF=44 is presumably the ancestral condition from which the remaining cytotypes evolved via Robertsonian autosomal fusions, a tandem fusion between a heterochromosome and an autosome, and pericentric inversion of heterosomes (Giagia-Athanasopoulou et al. 1995, Giagia-Athanasopoulou & Stamatopoulos 1997).

Variation and subspecies. High interpopulation variation, as retrieved in the karyotype (cf. above), allozymes (Nikoletopoulos et al. 1992, Tsekoura et al. 2002) and in nucleotide sequences (Thanou et al. 2012, Rovatsos & Giagia-Athanasopoulou 2012) is in sharp contrast with low overall craniometric variability (Tsekoura et al. 2002). Kratochvíl (1971) had previously noted that much of the reported cranial differentiation between the topotypes of *thomasi* and *atticus* is due to individual variation and Ondrias (1966) pooled all samples from Greece into a single subspecies. Phylogenetic reconstructions retrieved two lineages which were classified as distinct subspecies, *thomasi* and *atticus* (Thanou et al. 2012). In the results published by Tsekoura et al. (2002), craniometric analysis failed to separate these taxa. Since various characteristics vary independently, we hesitate to recognize subspecies. Size declines in a north-to-south direction.

Microtus felteni (Malec & Storch, 1963) – Balkan Pine Vole

Pitymys savii felteni Malec & Storch, 1963:171. Type locality: "Trnovo, 1200 m, Macedonia, Yugoslavia." Now North Macedonia.

Taxonomy. Described as a subspecies of *savii* and elevated to a full species on the basis of its distinctive karyotype (Petrov et al. 1976). Species status confirmed in nucleotide sequence analyses (Thanou et al. 2012). Traditionally classified in the *savii* species group along with *savii* and *pyrenaicus* (Chaline et al. 1988, Musser & Carleton 2005). According to available molecular evidence, *felteni* is putatively a sister species to *thomasi* (Martínková & Moravec 2012; disclaimed by Thanou et al. 2012).

Distribution. (Figure 292). West-central Balkan Peninsula in southern Serbia, North Macedonia, Albania, and north-western Greece (as far south as Epirus). The area of distribution measures 39,150 km^2 and the altitudinal range is 20–1,560 m, rarely up to 2,000 m. This vole has been captured in a variety of open habitats such as cultivations, meadows, shrubs, forest edges and clearings. Sympatric with *subterraneus* and *thomasi*; syntopic occurrence with the former is rare. The abundance of Balkan pine voles is low; in owl pellets from Albania, *felteni* is 30-times rarer than the more fossorial *thomasi* (Bego et al. 2008).

Characteristics. A small pine vole externally resembling *subterraneus*; the tail is on average shorter (TL/H&B=0.25–0.33) and the ears are decidedly smaller. Dimensions: BWt=16–28 g, H&B=83–105 mm, TL=23–39 mm, HF=14–15.7 mm, EL=6.4–8.5 mm, CbL=22.2–23.9 mm, ZgW=13.0–14.9 mm, MxT=5.5–6.5 mm. There are 5 plantar pads (Figure 263d) and 2 pairs of inguinal nipples. Dorsal fur is 7–8 mm long and the protruding hairs are at most 1.5 mm longer; tail is sparsely hairy and the terminal tuft is feeble (length=1.5 mm). Back is brownish buff or brown; belly is grey, washed by slate hair bases. Feet are whitish to brownish grey and the tail is variable, light or grey. The skull is flattened with a relatively long braincase, short rostrum and wide zygoma (ZgW/CbL=0.58–0.64); the interorbital region is broad and flat, and the bullae are swollen; incisive foramens are short but wide. Incisors are orthodont (Figure 289). M^3 is essentially as in *thomasi*, however the dental fields of the triangles are more frequently closed; T2–T3 are isolated in ~¾ of cases and T4 is closed in ~⅔ of individuals; rarely are T3–T4 confluent. Furthermore, the posterior cap tends to be longer and narrower and the postero-lingual re-entrant fold LR4 is present in >80% of molars. Karyotype: 2n=54, NF$_a$=54 (Petrov et al. 1976), the X chromosome is the largest acrocentric; the Y chromosome is medium to large acrocentric and fully heterochromatic (Mitsainas et al. 2010).

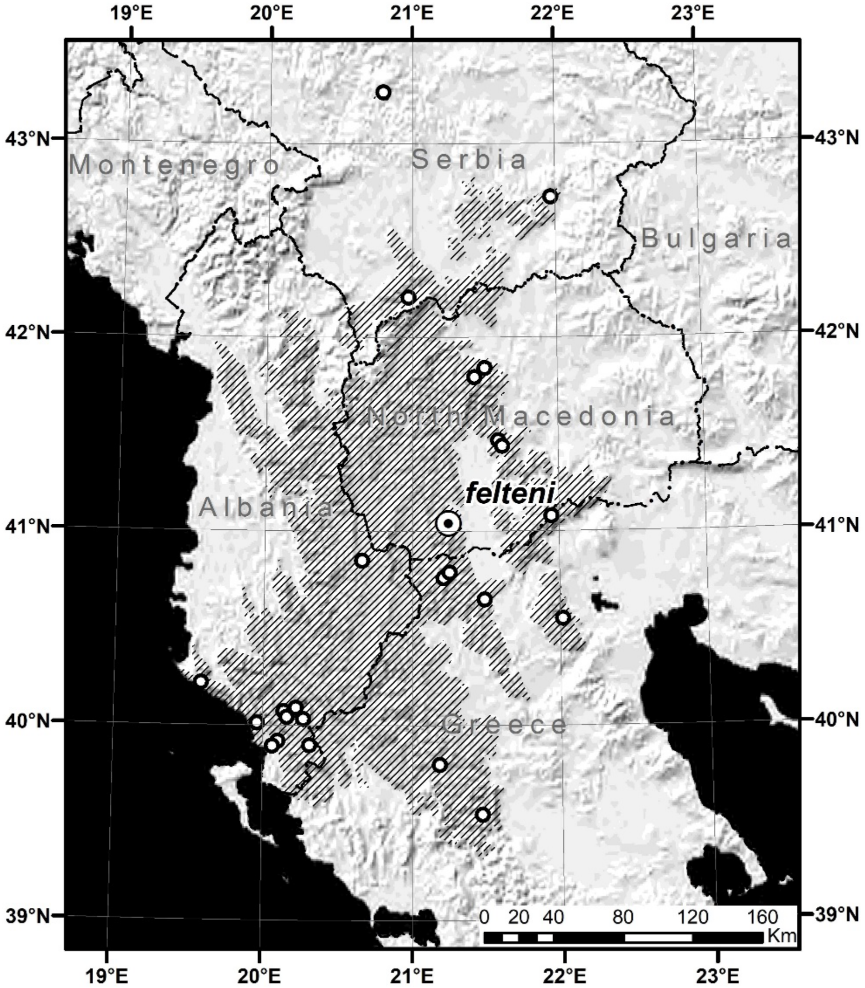


Figure 292: Distributional range of the Balkan pine vole *Microtus felteni*.

Variation and subspecies. Monotypic. Despite this, intraspecific genetic differentiation is high, possibly due to limited gene-flow between population fragments (Thanou et al. 2012).

SUBGENUS: *Microtus* Schrank, 1798 – Grey Voles

Microtus Schrank, 1798:72. Type species is *[Mus] "arvalis* Pallas" by subsequent designation (Miller 1896:14). See below.

Synonyms. *Campicola* Schulze, 1890 [preoccupied by Swainson 1827, for Aves]; *Campicoloma* Strand, 1928 [new name for *Campicola* Schulze)]; *Sumeriomys* Argyropulo, 1933; *Arvalomys* Chaline, 1974; *Hyrcanicola* Nadachowski, 2007.

Nomenclature. Validity of Miller's fixation of "*Microtus terrestris Schrank = Mus arvalis Pallas*" as the type species of *Microtus* Schrank (Miller 1896:14) is questioned by Russian authors. Malygin & Yatsenko (1986:584) stated that "*Microtus terrestris* Schrank, 1798, or more precisely, *M. terrestris sensu* Schrank, 1798" is not an available name (repeated in Pavlinov & Rossolimo 1987:190). The issue is discussed in Pavlinov & Lyssenko (2012:268) who concluded that "no type species appeared to be validly defined for the genus *Microtus* Schrank". This controversy requires clarification and below we summarise the nomenclatural history of the type fixation.

Schrank (1798:71–72) divided rodents ("Nager"; which also included Lagomorpha) into 8 genera. Three species of "Kleinohr" (German for "short-eared") were classified in a newly established genus *Microtus* (pp. 72–73): (i) *Microtus terrestris* with reference to "*Mus terrestris* Linnaeus, 1761:12" [correctly *Mus terrestris* Linnaeus, 1758:61] and with German vernacular Feldmaus, (ii) *Microtus amphibius* ("*Mus amphibius* Linnaeus, 1758:61") with German vernacular Waſsermaus, and (iii) *Microtus gregarius* ("*Mus gregarius* Linnæus, 1766:84") with German vernacular Reutmaus. Two of these names, *terrestris* and *amphibius,* are currently in *Arvicola amphibius* and *gregarius* is a synonym of *Microtus agrestis* Linnaeus.

Lataste (1883a) designated "*terrestris* L. et *arvalis* Pallas" as the type species for the genus *Microtus* (p. 348), and *arvalis* Pallas as the type species for the subgenus *Microtus* (p. 349). *Mus arvalis* Pallas was not originally included in *Microtus* as a nominal species and therefore cannot be fixed as its type species. Miller (1896:14) however concluded that "The *Microtus terrestris* of Schrank is not the *Mus terrestris* of Linnaeus, but the common field mouse of Central Europe, *Microtus arvalis* (Pallas)". With this, Miller corrected Schrank's earlier misidentification of "Feldmaus". As Miller fixed "the taxonomic species [*Mus arvalis* Pallas] actually involved in the misidentification" "and cite[d] together both the name previously cited as type species [*Microtus terrestris* Linnaeus] and the name of the species selected [*Mus arvalis* Pallas]" (cf. Art. 70.3 of the Code) his nomenclatural act is valid. The type species of *Microtus* is *Mus arvalis* Pallas, 1779 by subsequent designation (Miller 1896:14). *Microtus arvalis* Schrank is not an available taxonomic name.

Taxonomy. Microtus s.str. contains three major lineages which are occasionally classified as distinct subgenera (*Sumeriomys* and *Hyrcanicola*). Based on topology of phylogenetic trees and corresponding genetic distances (e.g. Steppan & Schenk 2017) we rank these lineages as species groups.

Distribution. Grey voles occupy temperate and boreal zones of Europe and Asia from the Atlantic coast of Europe and the North-African Cyrenaica, to the upper reaches of the Ob' and Irtysh Rivers, north-western Mongolia and northern Xinjiang. Altitudinal range is from sea level up to 4,500 m.

Characteristics. Small to large voles with tail shorter than ½ the head and body. There are 5–6 plantar pads. The posterolateral glands are on the hips, baculum is of trident type and the distal digits ossify; females have 8 nipples. Molars are frequently complex, i.e. M^3 with 4 inner and 3 outer salient angles and M_1 with a trefoil (consisting of confluent AC and T6–T7) anterior to triangles T4–T5; the latter are either confluent or alternating.

Species group *arvalis* – Grey Voles

Taxonomy. Ellerman (1941) was perhaps the first to use the *arvalis* group as a collective name for grey voles but this has only become common practice since the 1980s (Pavlinov & Roosolimo 1987, Zagorodnyuk 1990, and subsequent authors). In the past some species of *Alexandromys* (particularly *mongolicus*) were also classified in the *arvalis* group (see under *Alexandromys*).

Grey voles are a cluster of morphologically cryptic species hence their real taxonomic diversity became apparent through karyological research (Meyer et al. 1969, etc.). Experimental hybridisation played an important role in this phase of taxonomic and evolutionary research (reviewed in Sokolov & Bashenina 1994, and Meyer et al. 1996) and was combined with studies on copulatory behaviour (Zorenko & Malygin 1984, Sokolov & Bashenina 1994). With the exception of *arvalis* and *obscurus* pairing, the interspecific hybrids are sterile. Spermatoids do not develop to spermatozoa in hybrid males. There are also differences between species in copulatory behaviour, specifically in the number of thrusts. Since 2010, the species limits were further refined with *Cytb* phylogenetic reconstructions (Tougard et al. 2013, Mahmoudi et al. 2017a, Golenishchev et al. 2019) which resulted in the current 7 species. The group was reviewed in great detail in Russian literature (Malygin 1983, Meyer et al. 1996, Sokolov & Bashenina 1994).

The *arvalis* group holds a sister position with respect to social voles. Using the mutation rate for *Cytb* (Martínková et al. 2013), Mahmoudi et al. (2017a)

Figure 293: Representatives of grey voles: a–*Microtus arvalis* from the Czech Republic; b–*M. rossiaemeridionalis* from European Russia; c, d–*M. obscurus* from east Turkey (c) and Armenia (d). Photo by Miloš Anděra (a), Olga V. Osipova (b), Ahmet Karataş (c), and Boris Kryštufek (d).

estimated TMRCA of grey and social voles at 0.338 Mya. Approximations based on fossil calibration points, which are problematic in our opinion, yielded more ancient estimates (Tougard et al. 2013, Holicová et al. 2018).

Distribution. Temperate and boreal zones of Europe and Asia between the Atlantic coast in the west, as far east as the Zavkhan region in western Mongolia, the upper reaches of the Ob' and Irtysh Rivers and north-western Xinjiang. The northernmost records of occurrence are in southern Finland and the southernmost are in Zagros and Kerman (Iran). Thanks to human-facilitated transportation, *M. rossiaemeridionalis* significantly expanded its range in the last decades and reached Svalbard Islands (Arctic Ocean) in the north, and the Pacific coast in the east. Grey voles occupy structurally simple grassy and herbaceous habitats from sea level up to 4,500 m a.s.l.; in arid regions they frequently associate with the banks of bodies of water.

Characteristics (Figure 293). Small to large common voles with the tail shorter than ½ the length of head and body. The snout is blunt, the eyes are of modest size for arvicolines, and the ears protrude above the fur; their meatal lobe is low. Fur is soft to rather coarse, yellowish brown to dark brown above with variable effect of grizzling; flanks are usually lighter and demarcation towards the grey belly is frequently blurred. A colorimetric study showed great overlap between species; in pairwise interspecific comparisons >60% of individuals have identical colouration (Meyer et al. 1996). Juvenile voles are duller. There are usually 5 palmar and 6 plantar pads (Figure 294). Meyer et al. (1996) found 5 plantar pads only rarely in *arvalis-obscurus* and *transcaspicus,* and in ~10% of *rossiaemeridionalis* and *ilaeus*; deviation from 6 pads is frequently associated with an asymmetric number (5 and 6 pads in the same animal). Females have 8 nipples. Skull has rather widely expanded zygomatic arches (ZgW/CbL=0.53–0.63), narrow interorbital region, relatively deep braincase, and bullae of modest size. Adult skulls are ridged on the braincase and with prominent sagittal crest. The alveolar process on the outer side of the mandibular ramus is usually feeble. The upper incisors are orthodont. Molar pattern does not deviate from the average in the genus. M^2 normally lacks the postero-lingual salient angle LS4 (T5), and the M^3 usually has 4 inner and 3 outer salient angles. M^1 typically shows 5 alternating triangles and the anterior trefoil (AC and T6–T7). The baculum is of trident type. Sperm head is sickle-shaped and 1.8–2.4-times longer than wide, regardless of the species (Aksenova 1978). Nearly all species recognised here (5 out of a total of 7) differ in conventionally stained karyotype; ranges for diploid number and fundamental number of chromosomal arms are 2n=46–54 and NF=56–84, respectively. Main mechanisms of chromosomal change were centric fusions and pericentric inversions (Orlov & Malygin 1974).

Key to species

1a) M^3 shorter than M^1 with 3 inner salient angles; sutura naso-frontalis broad; 2n=52 ………………………………………… *transcaspicus*
1b) M^3 of about same length as M^1 or longer, usually with 4 inner salient angles; sutura naso-frontalis not broad; 2n either 46 or 54 ………………………….... 2
2a) 2n=46[*]……………………………………….... 3
2b) 2n=54[*] ……………………………………….. 4
3a) All autosomes are bi-armed; pelage is frequently with yellowish or buff tints; present west of ~43^0 east longitude ……………………………………… *arvalis*
3b) Karyotype includes 10 pairs of small acrocentric chromosomes; Pelage usually dull, without yellowish or buff tints; present east of ~37^0 east longitude (also in Crimea) ………………………………….… *obscurus*
4a) Present in Iran east of Lake Urmia …………..... 5
4b) Present elsewhere (in Iran west of Lake Urmia) ………………………………………………………. 6
5a) Smaller: HF<19 mm, CbL<27 mm, MxT<6.9 mm ………………………………………………… *mystacinus*
5b) Larger: HF>19 mm, CbL>27 mm, MxT>6.9 mm ………………………………………………… *kermanensis*
6a) $NF_a=72$; nasals shorter (<⅓ the skull length); present east of 58th meridian …………………… *ilaeus*
6b) $NF_a=54$; nasals shorter (~⅓ the skull length); present west of 58th meridian[**]…….... *rossiaemeridionalis*

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[*] M. arvalis-obscurus have smaller spermatozoid head than M. rossiaemeridionalis; cut-off point is 7.7 µm for length and 3.85 µm for width (Aksenova 1978)

[**] Recently translocated east of 58th meridian but all introductions are to the north of ~50th parallel; *M. ilaeus* is present south of 47th parallel

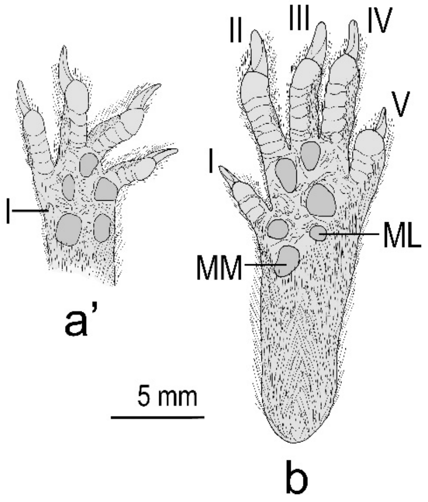


Figure 294: Left palm (a) and sole (b) in *Microtus arvalis* (a–Tomislavgrad, Bosnia and Herzegovina) and *M. rossiaemeridionalis* (b–near Bitola, North Macedonia).

Subgroup *arvalis*

The subgroup contains 2 parapatric species which share an identical diploid number of chromosomes (2n=46) but differ in the number of autosomal arms. These species are occasionally relegated to cytotypes.

Microtus arvalis (Pallas, 1779) – Common Grey Vole (Common Vole)

Mus (arvalis) Pallas, 1779:78. Type locality ("Per omnem Europam & Ruſſiam") was subsequently restricted to "Germany" (Miller 1912a:683). Designation of the neotype fixed the type locality to "Leningrad Oblast, neighbourhood of the town Pushkin" (Meyer et al. 1972:159), now the Pushkinsky

District of the federal city of St. Petersburg, Russian Federation.

Synonyms. *S[palax] minor* Leske, 1779; *Microtus terrestris:* Schrank, 1798 [not an available name; see the account on Nomenclature below]; *M[us] arv[alis] albus* Bechstein, 1801 [valid with reference to Articles 45.6.3&4 of the Code]; *Lemmus fulvus* É. Geoffroy Saint-Hilaire, 1803; *Lemmus fulvus* Sonnini, 1816 [first valid publication of *fulvus* Saint-Hilaire]; *Arvicola vulgaris* Desmarest, 1822 [nomen oblitum]: *Lemmus pratensis* Baillon, 1834; *Arvicola arvensis* Schinz, 1840 [substitute name for *arvalis*]; *Arv[icola] incertus* Sélys, 1841 [nomen dubium; cf. Niethammer & Krapp 1982:300, 422); *Arvicola pratensis* F. Cuvier, 1842; [subjective synonym of *Lemmus pratensis* Baillon]; *A[rvicola] incertus* Aberr. *albomaculatus* Selys, 1845 [nomen nudum]; *A[rvicola] arvalis* Aberr. *isabellinus* Selys, 1845 [nomen nudum]; *[Arvicola arvalis]* Var. *albus* Lesson, 1842 [nomen nudum; homonym of *albus* Bechstein]; *[Arvicola arvalis]* Var. *ater* Lesson, 1842 [nomen nudum]; *[Arvicola arvalis]* Var. *maculatus* Lesson, 1842 [nomen nudum]; *H[ypudaeus] rufescente fuscus* Schinz, 1845; *H[ypudaeus] rufo fuscus* Schinz, 1845 [nomen nudum]; *A[rvicola] cunicularius* Ray, 1847; *Arv[icola] arvalis* Var. *fulva* Fatio, 1869 [predated by *fulvus* Sonnini, 1816]; *M[icrotus] campestris brachyuros* König-Warthausen, 1875 [nomen nudum]; *Hypudaeos* [sic] *macrourus* König-Warthausen, 1875 [nomen nudum]; *Microtus orcadensis* Millais, 1904; *Microtus orcadensis sandayensis* Millais, 1905; *[Arvicola arvalis]* Var. *flava* Fatio, 1905 [renaming of *fulva* Fatio]; *Arvicola arvalis, Galliardi* Fatio, 1905; *A[rvicola] arvalis* forma *simplex* Rörig & Börner, 1907; *[Arvicola arvalis]* f[orma] *typica* Rörig & Börner, 1907; *[Arvicola arvalis]* f[orma] *duplicata* Rörig & Börner, 1907; *[Arvicola arvalis]* f[orma] *variabilis* Rörig & Börner, 1907; *[Arvicola arvalis]* f[orma] *contigua* Rörig & Börner, 1907; *[Arvicola arvalis]* forma *depressa* Rörig & Börner, 1907; *Arvicola arvalis* (Pall.) forma *assimilis* Rörig & Börner, 1907; *[Arvicola campestris]* f[orma] *maskii* Rörig & Börner, 1907; *[Arvicola arvalis]* Forma *principalis* Rörig & Börner, 1907; *Microtus levis* Miller, 1908; *Microtus arvalis meridianus* Miller, 1908; *Microtus asturianus* Miller, 1908; *Microtus angularis* Miller, 1908; *Microtus sandayensis westræ* Miller, 1908; *Microtus sarnius* Miller 1909; *M[icrotus] orcadensis ronaldshaiensis* Hinton, 1913; *Microtus orcadensis rousaiensis* Hinton, 1913; *Microtus arvalis calypsus* Montagu, 1923; *Microtus arvalis Havelkae* Bolkay, 1925; *Microtus arvalis Hawelkae* Bolkay, 1925 [emendation of *Havelkae* Bolkay; in corrigenda]; *Microtus arvalis Brauneri*

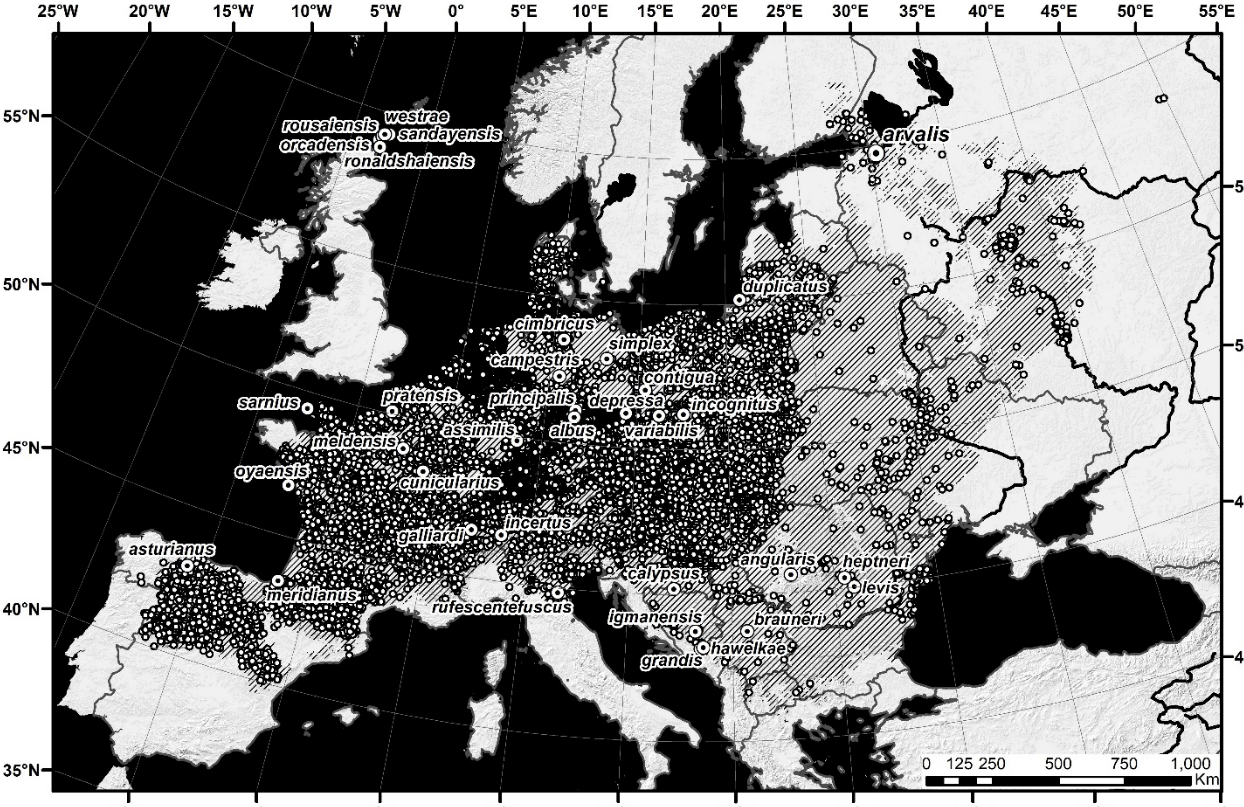


Figure 295: Distributional range of the common grey vole *Microtus arvalis*.

V. Martino & E. Martino, 1926; *Microtus igmanensis* Bolkay, 1929; *Microtus arvalis cimbricus* Stein, 1931; *Microtus arvalis incognitus* Stein, 1931; *Microtus arvalis oyænsis* Haim de Balsac, 1940; *Microtus arvalis grandis* V. Martino & E. Martino, 1948; *Microtus arvalis meldensis* Delost, 1955; *[Microtus arvalis] karamani* Kratochvil, 1959 [nomen nudum]; *Microtus arvalis heptneri* Hamar, 1963.

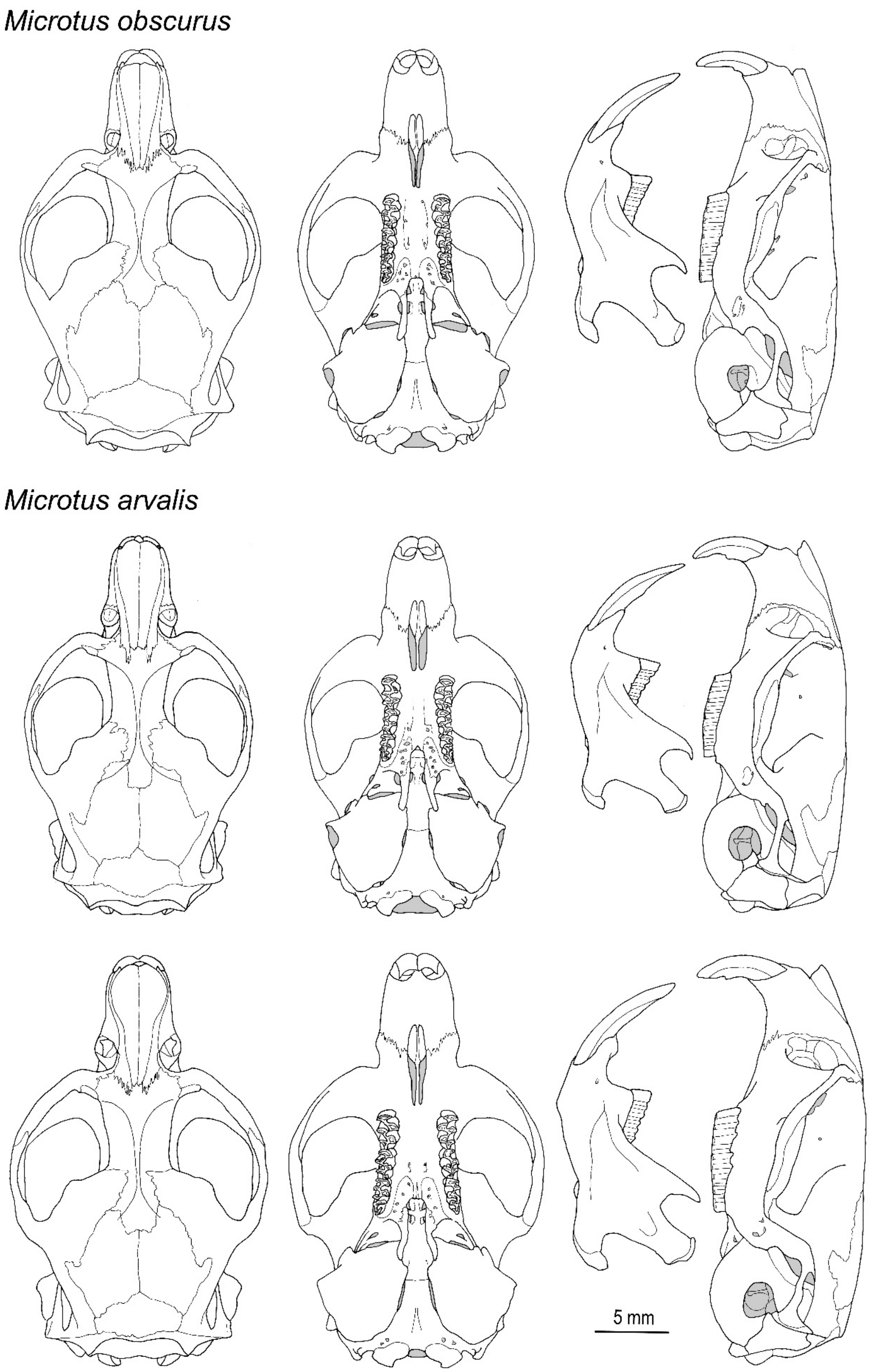
Taxonomy. In the opinion of many authors, *arvalis* and *obscurus* are conspecific (see the account on *obscurus*).

Common grey voles from the high altitudes of the Alps (1,400–1,800 m) in eastern France, Switzerland and western Austria were reported in the past as *incertus* (more rarely *rufescentefuscus;* both names are of doubtful application) and was still classified as a species in its own right in the 1980s (Fayard 1984). Miller (1912a:690) diagnosed *incertus* by cranial traits which suggested a more fossorial lifestyle, but Prescott-Allen (1971) found no evidence for 2 distinct morphotypes in Switzerland. Neither was *incertus* confirmed in crossbreeding trials (Matthey 1956) or by genetic evidence (García et al. 2020).

Distribution (Figure 295). Endemic to Europe: Spain north of the Tajo River (Aragón, Asturias, Bragança, Cantabria, Castilla y León, Castilla-La Mancha, Cataluña, Extremadura, La Rioja, Galicia, Madrid, Navarra, Valencia); Andorra; of very marginal presence in Portugal (Bragança Province); widespread in France (except western Bretagne and the Mediterranean coast) and further east across the mainland Europe north of the Alps (Low Countries, Germany, Denmark, Switzerland, Austria, the Czech Republic, Slovakia, Poland, Lithuania, Belarus, Hungary, Romania and Moldova). The north-western border is in Latvia and extreme southern Finland (Etelä-Suomen lääni). The southern border is in northern Italy (Emilia-Romagna, Friuli-Venezia Giulia, Lombardia, Piemonte, Trentino-Alto Adige, Valle d'Aosta, Veneto), along the East-Adriatic coast in Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, in the mountains of North Macedonia, and Bulgaria (where the range is still loosely documented). The eastern border is in Ukraine (to the line Odessa–Sumy Provinces) and western Russia between the upper Don and the upper Volga Rivers in the provinces of Nizhnii Novgorod, Ryazan, Tambov, Vladimir, Voronezh, and Yaroslavl'; in the north-east, there is an isolate in Vyatka (Kirov). Common grey voles are present on the Atlantic islands offshore France (Oléron, Aix, Normoutiere, Yeu; Fayard 1984), on Guernsey (Channel Islands), the Frisian (Wadden) Islands offshore the Netherlands (Texel, Vlieland, Terschelling, Ameland, and Schiermonnikoog; Haye & Jong 2003) and Germany (Baltrum, Wanderooge, Langeoog); in the North Sea offshore Germany (Nordstran, Pellworm, Sylt), and in the Baltic Sea off the coast of Germany (Fehrman, Nordstrand; Niethammer & Krapp 1982). Voles colonised the Dutch islands between the early 1870s and 2003 (Haye & Jong 2003) while the Orkney Islands were inhabited synchronously with humans (3.1–3.5 kya; Bayliss et al. 2017). In the Orkney archipelago (offshore northern Scotland), common voles are present on Westray, Sanday, Rousay, South Ronaldsay and Mainland Orkney; in 1940s they used a newly formed land-bridge and colonised Burray, and in the 1980s they were translocated from Westray to Eday; in the past, voles also lived on Holm of Papa and South Walls (Branscombe & Dobney 2016). The entire range measures 9,463,915 km^2.

Prime habitats are open cultivated farmland, fallow land, grazed pastures and turf meadows on deep soil; the common grey vole is able to live in poplar plantations, sand dunes, and hay meadows. Occupies altitudes from sea level up to ~3,000 m but is rare >2,000 m. A rapid (<20 years) range expansion of ~50,000 km^2 was reported in Spain (Luque-Larena et al. 2013).

Characteristics (Figure 293a). A grey vole of variable size with a short tail (TL=0.25–0.39). Dimensions: BWt=16–63 g, H&B=83–138 mm, TL=23–50 mm, HF=13–20 mm, EL=8–13.9 mm, CbL=22.2–30.1 mm, ZgW=13.2–17.8 mm, MxT=4.9–7.2 mm. Fur is soft and moderately long (=6.5–9 mm; protruding hairs measure 8–11.5 mm) and winter pelage is longer by ~40%; hairs on the tail do not conceal the annulation and the terminal pencil is short (2.5–5.5 mm). Colour varies individually and geographically. Upper parts are yellowish brown to dark brown with


Microtus obscurus

Microtus arvalis

Figure 296: Skull in grey voles: top–*Microtus obscurus* (Tcheremshansky District, Tatarstan, Russian Federation); middle–*M. arvalis* (near Ljubljana, Slovenia); bottom–*M. arvalis* (Mt. Prenj, Bosnia and Herzegovina).

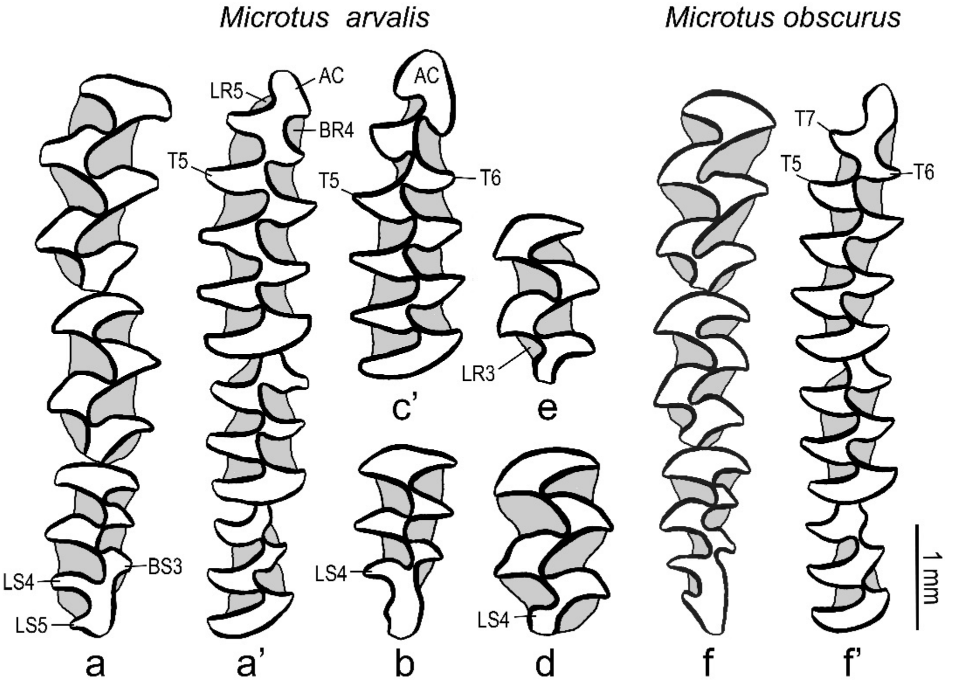


Figure 297: Molar pattern in grey voles. *Microtus arvalis*: upper (a) and lower row (a'–Schleswig-Holstein, Germany); isolated M³ (b–near Ljubljana, Slovenia); isolated M¹ (c'–and M² (c') (c',d,e–Cetinsko Polje, Dalmatia, Croatia). *M. obscurus*: upper (f) and lower row (f'–Aksunskyi, Arashan, Kyrgyzstan).

the variable effect of grizzling. The sides are frequently ochraceous-buff and the underparts are silvery grey to dull grey, always clouded by the slate-grey hair bases and commonly suffused with cream or buff shades; the belly frequently contrasts buffy flanks. The tail is usually inconspicuously bi-chromatic, brownish or blackish above and buffy or whitish below; feet are dull-whitish, buff, grey or brown. Aberrant colouration is covered in Frank & Zimmermann (1957; see also Reichstein 1957 and Humiński 1963). Skull has moderately expanded zygomatic arches; ZgW/CbL=0.53–0.63 (mean in 4 populations vary 0.58–0.61). Braincase is rather deep and well-ridged; sagittal crest is prominent. Bullae usually amount to ~⅓CbL (Figure 296). Upper incisors are orthodont, rarely slightly proodont. The molar pattern shows no peculiarities in the majority of voles, but individual and geographic variability is remarkable (see below). The M² usually lacks the postero-lingual salient angle LS4 (T5), and the M³ has 4 (rarely 3 or 5) inner and 3 outer salient angles; the 4th outer salient loop (BS4) is rare (present in 0.2% of voles from Central Europe; Uhlíková 2004) (Figure 297d). Re-entrant angles BR4–LR5 on M_1 are normally moderately deep and triangles T6–T7 are confluent with AC. In 12% of voles from Central Europe deep the re-entrant angles are deeper and isolate AC from triangles T6–T7 (Figure 297c'). Other morphotypes like the absence of BR4 (1%) or isolation of the dental field T6 (0.4%; Uhlíková 2004) are rare.

Length×width of the proximal baculum=1.75–2.80 × 1.05–1.85 mm; length of the distal baculum=0.50–1.25 mm (central digit) and 0.35–0.85 mm (lateral digit); the central digit is on average 1.5–1.8-times longer than the lateral digit (Aksenova 1980). Sperm head is of average size and smaller than in *rossiaemeridionalis*; length×width=6.48–7.92 × 3.15–3.78 µm (Aksenova 1978).

Since the late 1960s the karyotype of *M. arvalis* has attracted substantial interest and been intensely studied (summarised in Zima & Král 1984): 2n=46, NF=84; all autosomes and the X chromosome are bi-armed; the Y is acrocentric.

Variation and subspecies. A large number of subspecies was recognised in the past on the basis of colouration, size and molar morphotypes; a sizeable proportion of subspecies are insular races (*orcadensis, sandayensis, sarnius, oayensis*). Island populations, in particular those from Orkney, are the largest (mean

CbL=28.6 mm), followed by voles from the western Balkans (=26.7 mm) and Spain (=26.3 mm); the Central-European voles are the smallest (=24.2 mm in France). Size variation is considerable and was documented within subspecies (e.g. *asturianus*; Niethammer & Winking 1971), among habitats (Niethammer & Krapp 1982) and over time (Stein 1957); Corbet (1986) concluded that size bears little phylogenetic significance. Fur colouration does not show a geographic trend. The Orkney archipelago has both dark- (Mainland Orkney, South Ronaldsay, Rousay) and light-coloured voles (Westray, Sanday). A striking feature of morphological variability is the high proportion (60–90%) of the M^3 morphotype with 3 inner salient angles (simplex type; Figure 297b), which is restricted to the Baltic coast between the estuaries of the Elbe and Oder Rivers (northern Germany). The proportion of simplex molars remains high (>30%) between the estuary of the Weser River and the Gulf of Gdansk (a west-to-east distance of 650k m) and up to 150–200 km inland (Zimmermann 1935, Sałata 1974). The simplex morphotype is also reasonably frequent in voles from Yeu Island (46%) and locally in northern Spain (8–31%). In the majority of other populations a simple M^3 is seen in <10% of molars (summarised in Niethammer & Krapp 1982, Bekker 2020). Frequency of molar morphotypes was occasionally used in subspecies delimitation (Kratochvíl 1959). Spatial patterning is scale-dependant, as deduced from the frequency of polymorphic non-metric skeletal and dental traits. A meaningful pattern emerged in regional comparisons (Uhlíková 2004) but collapses on a large scale (Berry & Rose 1975). Prescott-Allen (1971:80) concluded that "morphological features in the common vole are influenced by so many factors that variation expressed by clear cut morphological patterns may occur only rarely, if at all."

Molecular screening retrieved two major groups of allopatric phylogenetic lineages which are further substructured (Bužan et al. 2010b, Martínková et al. 2013, García et al. 2020). The West-European group contains 3 lineages: (i) Iberian (Spain between Ebro and Tajo), (ii) Western-South (the Pyrenees and France between Ebro and Loire), and (iii) Western-North (France and western Germany between Loire and Rhine; also Orkney). The Central-Eastern group comprises 4 lineages: (i) Italian (southern Switzerland and northern Italy), (ii) Central (Switzerland, western Austria, Holland, Germany, Denmark), (iii) Eastern (east of the line N Adriatic–Oder River and north of the Balkan lineage), and (iv) the Balkan (southern Croatia, Bosnia and Herzegovina, Montenegro, Serbia, North Macedonia and likely Bulgaria). The current pattern is a legacy of the Last Glacial Maximum (LGM) and the Balkan lineage is the most divergent (García et al. 2020). Populations endured periods of adverse climate in glacial refugia and expanded when the climate ameliorated. During the post-LGM re-colonisation, which took place well into the Holocene, the phylogeographic lineages (specifically the Central and Eastern) expanded beyond their current ranges (Baca et al. 2020). Kratochvíl (1959) was perhaps the first to link the current infraspecific structuring in *arvalis* with survival in glacial refugia and subsequent re-colonisation.

Microtus obscurus (Eversmann, 1841) – Altai Grey Vole

Hypudaeus obscurus Eversmann, 1841:156. Type locality: "… montes altaicus [mountains of Altai]" restricted to the "valley of river Chuya" (Malygin & Yatsenko 1986:588), Russia.

Synonyms. *Microtus arvalis caucasicus* Satunin, 1896; *Microtus arvalis macrocranius* Ognev, 1924; *Microtus arvalis transcaucasicus* Ognev, 1924; *Microtus brevirostris* Ognev, 1924 [possibly a synonym of *obscurus*]; *Microtus arvalis gudauricus* Ognev, 1929; *Microtus arvalis transuralensis* Serebrennikov, 1929; *Microtus arvalis macrocranius* natio *ghalgai* Krassovsky, 1929; *Microtus arvalis iphigeniae* Heptner, 1946; *Microtus arvalis caspicus* Ognev, 1950 [synonymised with *obscurus* following our habitat modelling]; *Microtus arvalis ruthenus* Ognev, 1950; *Microtus arvalis innae* Ognev, 1950.

Nomenclature. Sherborn (1929:4489) quotes two 1841 papers by Eversmann, both announcing *obscurus* as a new name. The same paper was, in fact, published twice, firstly in the Proceedings of the Kazan University and afterwards as a separate fascicle with its own pagination. As the original publication was difficult to access, Dresser (1876) published a facsimile edition which is quoted by the majority of authors (the name is on p. 5).

Taxonomy. Hollister (1913:516) categorically claimed that *obscurus* "is an independent species, and not a race of *Microtus arvalis*", which was accepted by Allen (1924, 1940). This view however, was rare in the mid-20th century and the vast majority of authors synonymised *obscurus* with *arvalis*. Two cytotypes of the 2n=46 voles, differing in the NF (Orlov & Malygin 1969) provided grounds for the reinstallment of *obscurus* as a species in its own right (Zagorodnyuk 1991a,b) which slowly gained support.

M. obscurus and *arvalis* have allopatric ranges with very limited parapatric overlap. Hybridisation was reported from Belgorod–Voronezh–Lipetsk (Baskevich et al. 2005, 2012) and the Vladimir–Nizhny Novgorod regions (Meyer et al. 1997, Baskevich et al. 2016a) with the width of the hybrid (transgression) zone of >100km (Gromov et al. 2015). Inside the hybrid zone the proportion of voles with the recombinant karyotype is high but F1-hybrids are rare (Baskevich et al. 2012) and hybrids are frequently backcrosses with *M. obscurus* (Mironova et al. 2019). Interspecific hybrids develop normal synaptonemal complexes of bivalents and are fertile (Safronova et al. 2011) although Sablina (2015) reported on reduced litter size and partial male sterility in F2. TMRCA for *arvalis* and *obscurus* is putatively 0.184 Mya (Mahmoudi et al. 2017a).

Distribution (Figure 298). Range is of similar surface area (3,225,787 km^2) as in *arvalis*, but is shifted eastward and the two species are effectively allopatric. The range is largely contiguous between the lower Don River in the west and northern Xinjang and western Mongolia (Bayan-Ölgiy and Zavkhan) in the east, encompassing eastern Ukraine (Lugansk), Russian Federation (Kursk, Belgorod, Voronezh, Lipetsk, Vladimir, Nizhegorodskaya, Tambov, Kostroma, Penza, Saratov, Kostroma, Mari El, Ulyanovsk, Kirov, Samara, Arkhangels, Komi, Perm, Tatarstan, Bashkortostan, Chelyabinsk, Yekaterinburg, Kurgan, Tyumen', Omsk, Novosibirsk, Altai Krai, Altai Republic, and Kemerovo), and northern and eastern Kazakhstan (Altyrau, Aqtöbe, Qostanay, North Kazakhstan, Qaraghandy, Almaty, East Kazakhstan). The

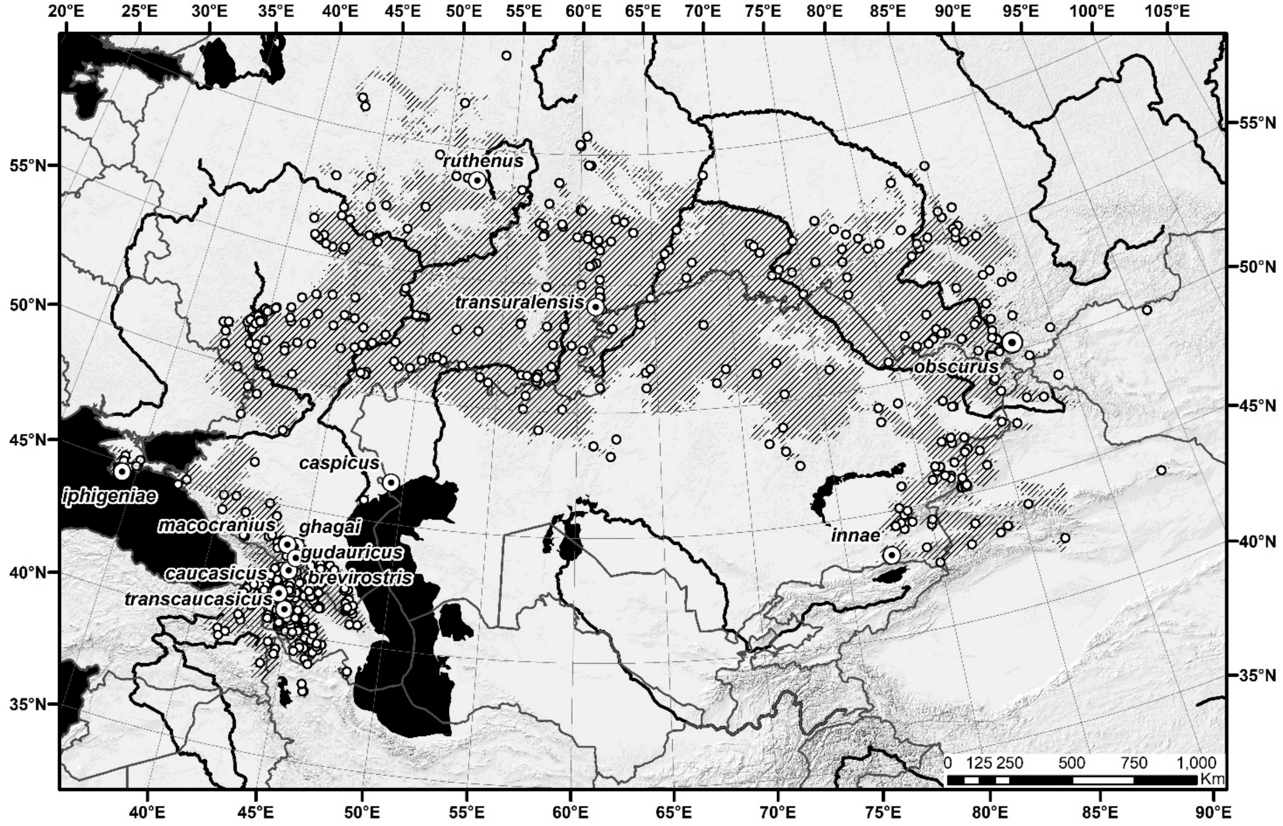


Figure 298: Distributional range of the Altay grey vole *Microtus obscurus*.

northernmost records are from Komi (63.55° northern latitude), Arkhangelsk (61.2°) and the Urals (60.7°). To the south of the Don River is a large isolate centred in the Caucasus which includes the provinces of south-western Russia (Rostov, Krasnodar, Stavropol', Adygeya, Karachayevo-Cherkesiya, Kabardino Balkarija, North Osetiya, Ingushetiya, Chechniya, and Dagestan), eastern Turkey (Ağrı, Ardahan, Kars, Erzurum, and Van), Georgia, Armenia, Azerbaijan, and north-western Iran (Azarbayjan-e-Gharbi and Azarbayjan-e-Sharqi). There are a further two isolates in this part of the range: (i) on Crimea and (ii) around Astrakhan.

The range is squeezed between the taiga zone in the north and the arid regions in the south. Main habitats are turf meadows, large tracts of ploughed and fallow farmland (e.g. Okulova et al. 2008) and alpine pastures in the south. Altitudinal range is from –27 m (Caspian Depression) to 3,035 m.

Characteristics (Figure 293c,d). Morphologically, *obscurus* is indistinguishable from *arvalis*. Size is moderate and tail is short (TL/H&B=0.26–0.41). Dimensions: BWt=21–62 g, H&B=95–136 mm, TL=31–52 mm, HF=13.6–20 mm, EL=8.9–15 mm, CbL=23.2–27.2 mm, ZgW=12.6–15.7 mm, MxT=5.0–6.8 mm. Fur is 6.5–11.5 mm long and rather rough; the protruding sparse hairs measure up to 9–14.5 mm; terminal pencil on the tail is 3–6 mm long. Pelage is usually dark brown and a buffy tint is rarely seen; *obscurus* never display the buffy-yellow dorsum which is frequent in *arvalis*. The belly is grey and lightened by a cream wash. The tail is grey-brown throughout or obscurely bi-chromatic, more blackish above. Feet are light-grey to brown and ears are grey. Skull is as in *arvalis*; ZgW/CbL=0.53–0.62 (Figure 296). Molars display a lower number of morphotypes than *arvalis* (Peskov & Tsudikova 1997); M^3 has 4 inner and 3 outer salient angles; the 4th outer salient angle BS4 is only rarely present (in ~15% of voles) and remains small; simplex morphotype (absent LS5) is rare (Figure 297f). M_1 shows little variation; the anterior cap is closed in ~½ of animals. Baculum is like in *arvalis*; length×width of the proximal bone=2.05–2.85 × 1.00–1.90 mm. Length of the distal baculum=0.70–1.30 mm (central digit) and 0.45–0.95 mm (lateral digit); central digit is on average 1.3–1.6-times longer than the lateral digit (Aksenova 1980). Karyotype: 2n=46, NF=72, NF_a=68; 12 autosomal pairs are bi-armed (including 1 subtelocentric pair) and 10 pairs are acrocentric. The X chromosome is metacentric and the Y is either bi-armed or acrocentric (Malygin 1983, Arslan & Zima 2014).

Variation and subspecies. Two major phylogenetic lineages (the widespread Sino-Russian and the Middle-Eastern) putatively diverged 0.119 Mya (Mahmoudi et al. 2017a); both show low genetic diversity (Tougard et al. 2013). The Middle-Eastern lineage was further split 59 kya into the Southern-Caucasian lineage and the Iranian lineage (Mahmoudi et al. 2017a).

Subspecific taxonomy is not elaborated. Ognev (1950) recognised 7 subspecies (the nominal, *macrocranius, gudauricus, transcaucasicus, iphigeniae, ruthenus, transuralensis*; all classified as *arvalis*) and Gromov & Erbajeva (1995) retained 5 (all except *ruthenus* and *transuralensis*). They are diagnosed by slight differences in average size and colouration. Dzuev et al. (2013) showed that two of the subspecies (*gudauricus* and *macrocranius*) also differ in litter size (smaller in *macrocranius*) and time of sexual maturity (postponed in *macrocranius*); they freely hybridise.

Subgroup *mystacinus*

The subgroup contains 3 species which share an identical diploid number of chromosomes (2n=54). A triple taxonomy (*rossiaemeridionalis*, *mystacinus* and *kermanensis*) follows the phylogenetic trees in Mahmoudi et al. (2017a) and Golenishchev et al. (2019) and the results of interspecific pairing. Hybrid males are invariably sterile, reportedly a consequence of chromosomal asynapses (Bikchurina et al. 2021); Zafronova et al (2011), however, found normal synaptonemal complexes of bivalents during meiosis in *rossiaemeridionalis* × *kermanensis* hybrids. The subgroup diversified in south-western Asia with diversity peaking in Iran.

Microtus rossiaemeridionalis Ognev, 1924 – East-European Grey Vole

Microtus arv[alis] rossiae-meridionalis Ognev, 1924: 27. Type locality: "Novii Kurlak, Bobrov subdistrict [uezd] of the Voronej Govt. [Voronezh Oblast]", Russian Federation.

Synonyms. *Microtus arvalis muhlisi* Neuhäuser, 1936; *Microtus arvalis relictus* Neuhäuser, 1936; *Microtus arvalis rhodopensis* Heinrich, 1936; *Microtus arvalis epiroticus* Ondrias, 1966; *Microtus subarvalis* Mejer, Orlov & Skholl, 1972 [preoccupied by *Microtus subarvalis* Heller, 1933]; *M*[*icrotus*] *r*[*ossiaemeridionalis*] *ponticus* Zagorodnjuk, 1993.

Taxonomy and nomenclature. The discovery of an entirely new species inside a thoroughly studied *M. arvalis* was a great surprise for Palaearctic mammalogists, even greater as no indices suggested such taxonomic complexity. A distinctive karyotype of the two morphologically cryptic species and their sympatry removed all doubts regarding their taxonomic status as independent species (Corbet 1978). While the 2n=46 chromosomal form was easily linked with *arvalis*, a search for the correct taxonomic name for the 2n=54 form was slow and painstaking (Malygin & Yatsenko 1986, Mazurok et al. 1995). The name *subarvalis* which Meyer et al. (1972) coined for the 2n=54 voles is preoccupied by *subarvalis* Heller (see above). Subsequent karyotyping throughout the grey voles' range uncovered two candidate names for the 54-chromosme voles: *epiroticus* Ondrias, 1966 (Ružić et al. 1975), and *rossiaemeridionalis* Ognev, 1924 (Malygin 1983); the latter holds priority over the former. After examining a skull of the type of *levis* Miller, 1908, Masing (1999) concluded that *levis* is conspecific with *rossiaemeridionalis* and its senior synonym. Zima et al. (1981) considered such a possibility but refrained from making a firm conclusion, and Kryštufek & Vohralík (2005:172) exposed uncertainties associated with Masing's interpretation. Furthermore, habitat modelling showed that the type locality for *levis* is outside the range of 54-chromosme voles but inside the range of *arvalis* (Mezhzherin et al. 2017; see also Figures 295 and 298). Topotypes of *levis* have thus far neither been karyotyped nor screened for molecular makeup. Ghorbani et al. (2015) showed that voles from northern Iran have 2n=54 chromosomes and Mahmoudi et al. (2017a) concluded that *mystacinus* Filippi is the oldest name for the East-European grey vole (followed in Pardiñas et al. 2017, Yusefi et al. 2019).

Various traits of external, cranial and dental morphology were proposed for separation between rossiaemeridionalis and *arvalis*. Classification of museum material which employed numerical taxonomy techniques yielded mistaken results (e.g. Markov et al. 2012). Kratochvil (1982, 1983) segregated crania of the two voles by the volume of the neurocranium relative to skull length (larger scores in *rossiaemeridionalis*). As subsequently confirmed by Yaskin & Lenetz (1996) *rossiaemeridionalis* has a larger brain mass (514±6.8 mg in males, 490±9.3 mg in females) than *arvalis* (458±6.6 mg and 442±8.4 mg, respectively). This trait, however, has never been widely used in routine classification of museum vouchers. Species differ categorically in size of spermatozoid head (larger in *rossiaemeridionalis*; Meyer et al. 1972, 1996).

Distribution (Figure 299). The native range (area=2,460,340 km^2) covers the south-eastern Balkans (southern Albania, southern Serbia, North Macedonia, northern Greece, and southern and eastern Bulgaria), the northern Black Sea coast (eastern Romania, Moldova and southern Ukraine), and a wide belt between the Don and Ural Rivers, eastern Belarus (Mogilev), eastern Ukraine (Cherkassy, Dniepropetrovsk, Donets'k, Khar'kov, Kherson, Kiev, Kirovograd, Luhansk, Nikolayev, Odessa, Sumy, Zaporizhzhia, Zhitomir), Russian Federation (Moscow, Tula, Belgorod, Kursk, Voronezh, Lipetsk, Yaroslavl', Stavropol', Tambov, Rostov, Volgograd, Saratov, Penza, Nizhniy Novgorod, Mari El, Tatarstan, Samara, Orenburg, N Krasnodar, Kalmykiya, Astrakhan'), and western Kazakhstan (Aqtöbe, Atyrau, West Kazakhstan, Kustanay). The east-European grey vole is largely absent between the Black Sea and the Caspian Sea, except for Dagestan, but is present again to the south of the Caucasus throughout Turkey (except the south-eastern lowlands), adjacent Armenia (Ararat) and north-

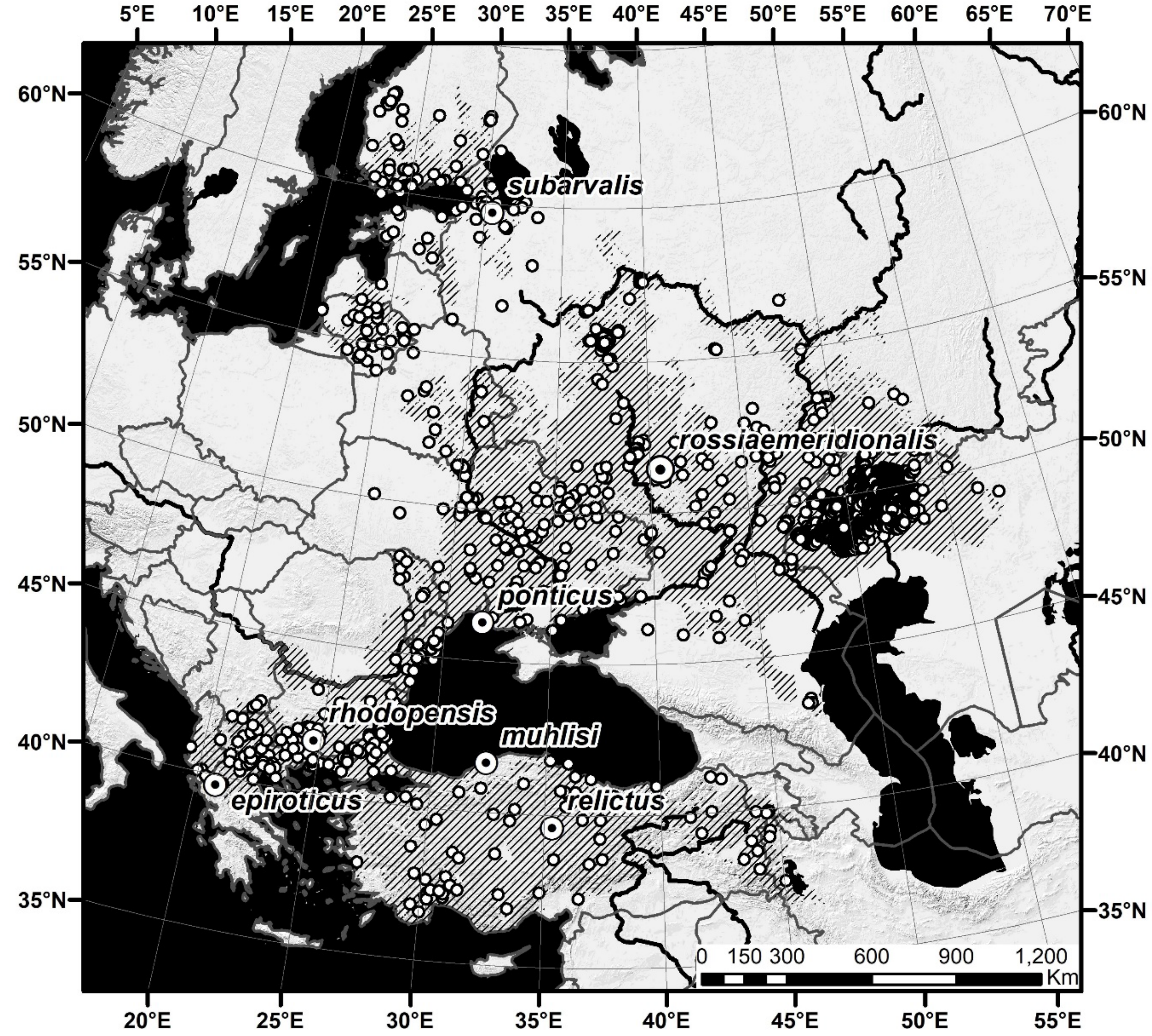


Figure 299: Distributional range of the East-European grey vole *Microtus rossiaemeridionalis*.

western Iran (Azarbayjan-e-Gharbi). Isolated populations of varying size are scattered along the western and north-western range edge in western Ukraine (Khmel'nitskaya, Ternopol'), Belarus (Homel and Minsk), Lithuania (Alytaus, Kauno, Klaipedos, Marijampoles, Panevezio, Siauliu, Utenos, Vilniaus), Latvia (Riga), Estonia (Harjumaa, Ida-Virumaa, Jïgevamaa, Pïlvamaa, Raplamaa, Tartumaa), north-eastern Russia (Kareliya, Leningrad, Novgorod), and southern Finland (as far north as 63.1° northern latitude). The vertical range occupied by *M. rossiaemeridionalis* is from –27 m (Caspian Depression) to 3,250 m.

In contrast to *arvalis* and *obscurus, rossiaemeridionalis* is rare in agricultural land and mown fields and prefers cover of tall and dense herbs and grasses, and frequents the shores of water bodies. It can be found in settled areas (parks and gardens), in haystacks and even inside storage sheds where harvested crops are kept. In many places, *rossiaemeridionalis* is sympatric with either *arvalis* or *obscurus;* e.g. in Baltic countries (Mažeitkytė et al. 1999) and between the Don and Ural Rivers (Karaseva et al. 1995, Okulova et al. 2008).

The Eastern grey vole has remarkable invasive potential and during the late 20th century expanded its range border by ~1,500 km northward and ~6,500 km eastward, reaching the Svalbard Islands in the Arctic Ocean and the Pacific Ocean in the Russian Far East (Figure 300). In European Russia, isolated populations are known from Murmansk, Vologda, and Komi in the north and from Crimea and Krasnodar in the south. Introduced populations have been recorded in numerous places to the east of the Volga and Kama Rivers in Bashkortostan, Yekaterinburg, Chelyabinsk, Kurgan, Tyumen, Khanty-Mansiyskiy, Novosibirsk, Tomsk, Khakasiya, Irkutsk, Buryatiya, Khabarovsk, and Eastern Kazakhstan. It is not clear for all populations whether they are native or imported (cf. Malygin et al. 2020 and Holicová et al. 2018). Most Siberian localities, however, are along the Trans-Siberian railroad which speaks in favour of human-assissted spreading. The earliest translocation was likely to Svalbard (<1960) and was followed by the introduction of *rossiaemeridionalis* to Baikal in the late 1970s. Reports on the East-European grey vole outside its native range started to become frequent in the late 1980s (reviewed in Malygin et al. 2020). Voles were obviously passively transported, mostly hidden in cargo carried by supply ships and trains. Voles frequently settled in urban centres and rapidly spread in these novel environments. Inside the city of Irkutsk, they are the most abundant small mammals (Moroldoev et al. 2017). In Svalbard, where they are faced with the Arctic climate, voles thrive independently of humans in the natural environment on peat soil (Fredga et al. 1990). Malygin et al. (2020) suggested that the invasive potential of *M. rossiaemeridionalis* is due to the combination of ecological plasticity, docile behaviour, and resistance to low temperatures.

Characteristics (Figure 293b). Externally, cranially and dentally, *M. rossiaemeridionalis* is similar to *arvalis*. Tail is on average slightly more than ⅓ H&B (TL/H&B=0.28–0.42). Dimensions: BWt=21–58 g, H&B=96–130 mm, TL=31–55 mm, HF=14.4–19.7 mm, EL=9.2–13.8 mm, CbL=24.0–27.6 mm, ZgW=13.3–16.5 mm, MxT=5.5–6.9 mm. Although not evident from these data, several regional studies reported a relatively longer tail and longer hind foot in *rossiaemeridionalis* than in *arvalis* (Mažeitkytė et al. 1999) or *obscurus* (Kryštufek & Vohralík 2005). The skull differs from that of *arvalis-obscurus* in that: (i) zygomatic arches are on average less expanded; (ii) braincase is relatively longer; (iii) incisive foramina are shorter and broader; (iv) postorbital processes of squamosal bone is only rarely well-pronounced (Figure 301). Complex molar morphotypes are more common in *rossiaemeridionalis* than *arvalis-obscurus* (Peskov &

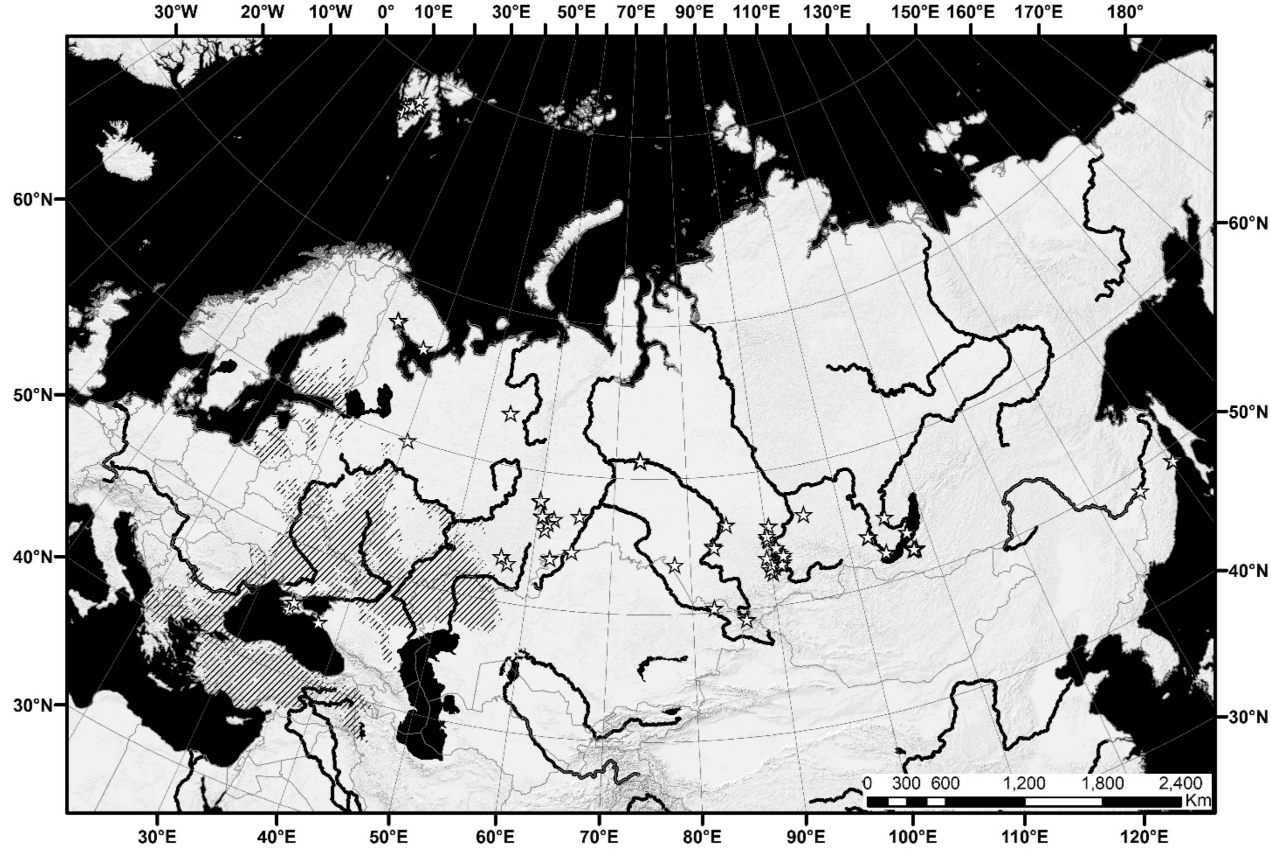


Figure 300: Native range of Microtus rossiaemeridionalis (shaded) and occurrences of introduced populations (stars).

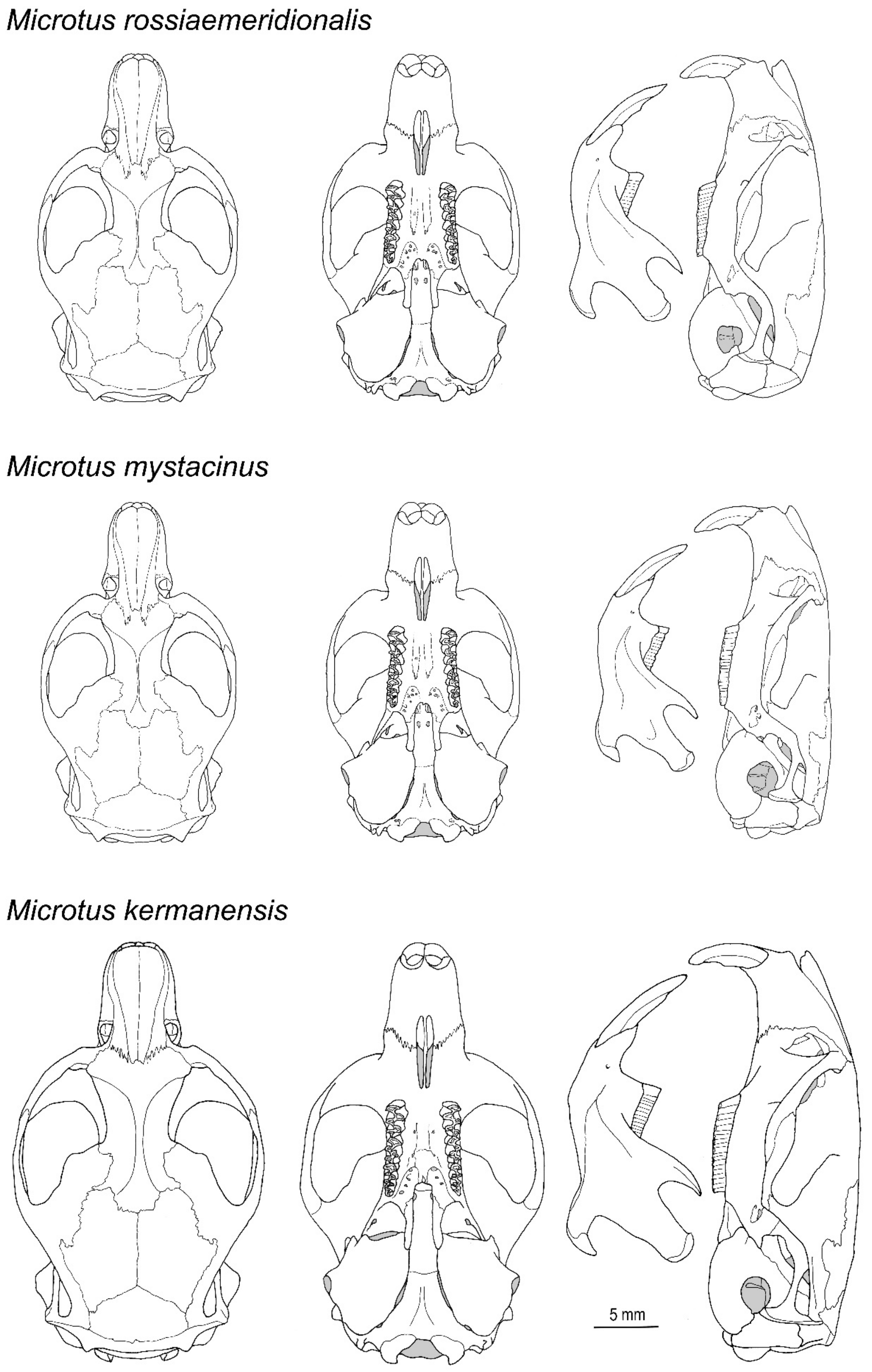


Figure 301: Skull in grey voles: top–*Microtus rossiaemeridionalis* (Karabulut, Konya, Turkey); middle–*M. mystacinus* (Semnan Province, Iran); bottom–*M. kermanensis* (Dzhiroft, Kerman Province, Iran).

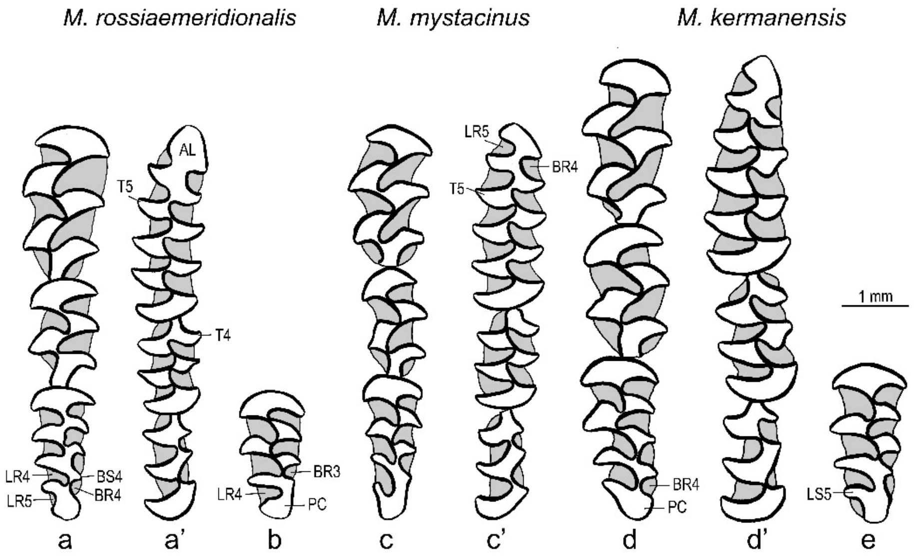


Figure 302: Enamel molar pattern in grey voles. *Microtus rossiaemeridionalis*: upper (a) and lower row (a'); isolated M³ (b–all from Konya, Turkey). *M. mystacinus*: upper (c) and lower row (c'–Soltanieh, Zanjan Province Iran). *M. kermanensis:* upper (d) and lower row (d'–from Dzhiroft, Kerman Province, Iran); isolated M³ (e–ssp. *kermanensis*, Dzhiroft).

Tsudikova 1997, Markova et al. 2003). The M^3 is more variable than the remaining molars with 4 inner and 3–4 outer salient angles; in Lithuania, 52% of voles display 3 outer salient angles and 38% show 4 angles (Mažeitkytė et al. 1999) while in the Balkans the majority have 3 outer angles. The posterior cap of M^3 starts posterior to T4 or T6. The M_1 nearly invariably displays 5 inner and 4 outer re-entrant angles (Figure 302). Baculum is as in *arvalis*; length×width of the proximal bone=1.90–2.60 × 0.85–1.70 mm. Length of distal baculum is 0.75–1.35 mm (central digit) and 0.55–1.20 mm (lateral digit); central digit is on average 1.05–1.54-times longer than the lateral digit (Aksenova 1980). Sperm head is the largest in the *arvalis* species group: length×width=7.74–9.72 × 3.50–4.95 µm (Aksenova 1978). Karyotype: 2n=54, NF_a=54 (Meyer et al. 1996, Arslan & Zima 2014, Selçuk & Kefelioğlu 2018). Sex chromosomes are acrocentric and of large size.

Variation and subspecies. Pardiñas et al. (2017) treated this vole as monotypic. Two allopatric *Cytb* lineages were retrieved. One lineage is restricted to Anatolia and is probably marginally present in southern Armenia and north-western Iran; the other lineage is widespread; TMRCA is 92 kya (Mahmoudi et al. 2017a).

Microtus mystacinus (Filippi, 1865) – Caspian Grey Vole

Ar[vicola] mystacinus Filippi, 1865:255. Type locality: "Valley of Lar", Northern Iran.

Synonyms. *Microtus hyrcania* Goodwin, 1940; *Microtus arvalis khorkoutensis* Goodwin, 1940.

Taxonomy. In the early 20th century *Arvicola mystacinus* was still regarded as a species in its own right (Cabrera Latorre 1901) but was subsequently synonymised with either *arvalis* (e.g. Lay 1967) or *socialis* (Corbet 1978). Lay and Corbet examined the same syntypes of *mystacinus* but reached different conclusions. After examining 1 of Filippi's syntypes, we are of the same mind as Lay and therefore classify *mystacinus* in the *arvalis* group. In recent years, *mystacinus* embraced all grey voles with 54 chromosomes (Pardiñas et al. 2017, Yusefi et al. 2019). Conclusive arguments for the current status stems from hybridisation trials (Bikchurina et al. 2021; see under species group). The species consists of 2 deeply divergent *Mt*-lineages (Mahmoudi et al. 2017a).

Several authors (Musser & Carleton 1993, 2005, Meyer et al. 1996) synonymised Goodwin's names *hyrcania*

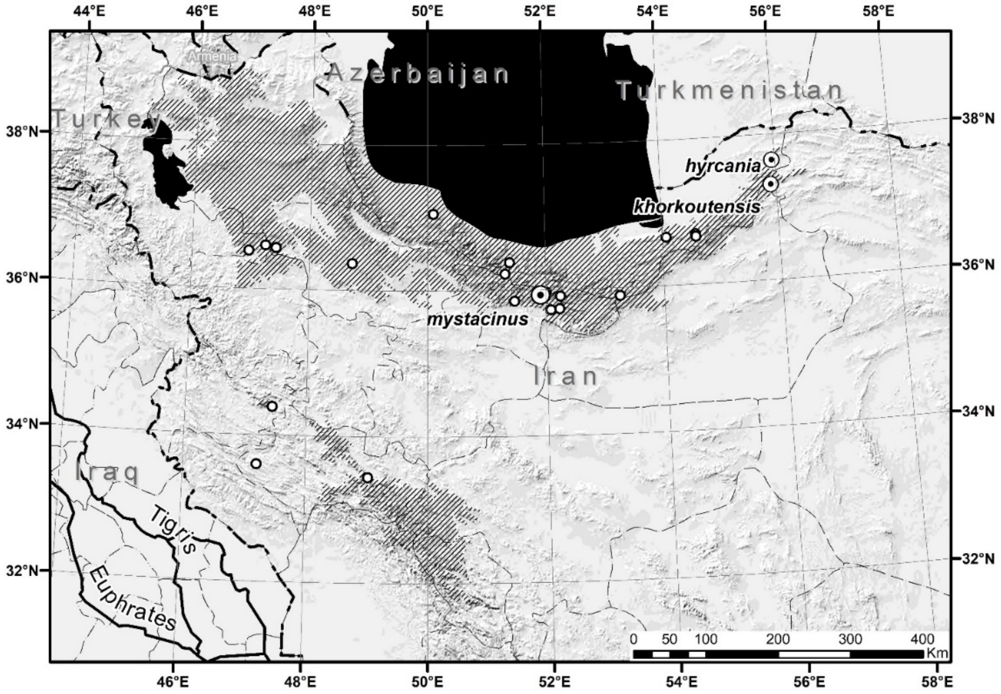


Figure 303: Distributional range of the Caspian grey vole *Microtus mystacinus*.

and *khorkoutensis* with *arvalis* s.lat. Type localities for both taxa are far outside the range for *obscurus* (cf. Mahmoudi et al. 2017a; Figures 295 & 298), therefore we list them as synonyms of *mystacinus*.

Distribution (Figure 303). Endemic to Iran. The range (area=144,225 km^2) is in 2 fragments. The most extensive is the northern fragment in Azarbayjan-e-Gharbi, Zanjan, Gilan, Mazanderan, Tehran, Semnan, and Golestan. The south-western fragment is known from 3 localities in the Zagros Mts. in Kermanshah and Lorestan. Voles occupy valleys, banks of irrigation channels and slopes, either forested or covered with brushes and clumps of grasses, usually in the mountains. Altitudinal range is 200–3,080 m.

Characteristic. Size is medium: BWt=18–26.5 g, H&B=93–135 mm, TL=30–42 mm, HF=16–18 mm, EL=10–15 mm, CbL=23.4–26.3 mm, ZgW=13.0–15.1 mm, MxT=5.2–6.6 mm. Tail is of average length (TL/H&B=0.31–0.39). Back is yellowish brown, grizzled by black tips of long protruding hairs; flanks are pale and more clearly ochraceous and the demarcation towards the belly is distinct; underside is dirty-white and shaded yellow with slate basal colour showing through. The tail is well-clothed in hair and indistinctly to sharply bi-chromatic, dark yellowish brown above and light buff bellow; feet are drab. Skull and dentition (Figures 301 & 302) are as in *rossiaemeridionals*; the alveolar process on the outer side of the mandibular ramus is moderately exposed. Karyotype: 2n=54, NF_a=54; both heterosomes are acrocentric (Ghorbani et al. 2015, Mahmoudi et al. 2018).

Variation and subspecies. *M. mystacinus* consists of 2 allopatric lineages: the Western (the western isolate to the west of Lar) and the Eastern (Lar and further east into Golestan); molecular makeup is not known for the Zagros fragment (Mahmoudi et al. 2017a).

Microtus kermanensis Roguin, 1988 – Kerman Grey Vole

Microtus kermanensis Roguin, 1988:601. Type locality: "Zahrud-e Bala, 70 km south of Kerman, 2700 m, north slope of Kuh-e Hazar. Coordinates: 29^{o}33' N-57^{o}19' E, Kerman Province, Iran".

Taxonomy. Musser & Carleton (2005) synonymised *kermanenis* with *transcaspicus*; these species differ in the shape of the naso-frontal suture and M^3 (Roguin 1988) and in karyotype (Mahmoudi et al. 2018).

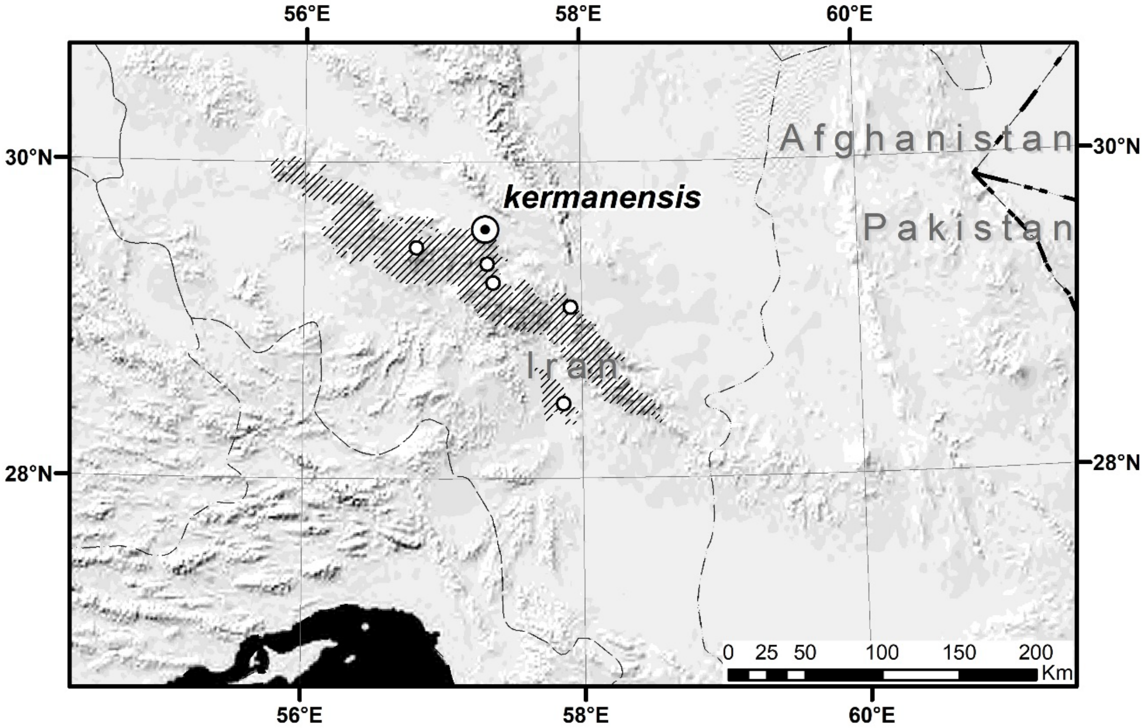


Figure 304: Distributional range of the Kerman grey vole *Microtus kermanensis*.

Distribution (Figure 304). Endemic to Kerman Province, south-eastern Iran. The range is an isolate of 10,320 km² inside the Iranian arid region. The vole closely associates with the banks of streams and irrigation channels. Elevational range is 600–3,250 m.

Description. Large and long-tailed voles (TL/H&B=0.28–0.44). Dimensions: BWt=41–57 g, H&B=114–152 mm, TL=43–54 mm, HF=20–23 mm, EL=13–16.1 mm, CbL=27.6–32.8 mm, ZgW=16.8–18.8 mm, MxT=7.0–8.1 mm. Back is grey-brown, grizzled by yellowish-brown hair tips; flanks are light grey, transition toward the belly is blurred. The underside is grey, shaded light beige; the throat is darker. Head is of the same colour as the back; snout is lightly rusty and ears are grey. Tail is densely clad with hairs; terminal brush measures 11–12 mm. The skull shows no peculiarities (Figure 301); zygomatic arches are moderately expanded (ZgW/CbL=0.54–0.61). The alveolar process on the outer side of the mandibular ramus is less exposed than in *mystacinus*. Molars are complex (Figure 302): M^3 has 3 deep inner and 3–4 outer re-entrant angles; M_1 has 5 inner and 4 outer re-entrant angles. The baculum is large; the proximal bone is 3.45–4.10 mm long and 2.35–2.65 mm wide across the basal expansion; the central distal baculum is relatively short (length=1.47–1.60 mm), i.e. 2.0–2.4-times longer than the lateral digit (estimated from a figure in Golenishchev et al. 1999).

Variation and subspecies. Monotypic.

Subgroup *transcaspicus*

Microtus transcaspicus Satunin, 1905 – Transcaspian Grey Vole

Microtus transcaspicus Satunin, 1905:57. Type locality: "Chuliyskoe ravin, of Transcaucasian Oblast", Geok Tepinsky raion, Ashgabad [now Ahal] Oblast, Turkmenistan.

Taxonomy. The majority of authors accepted *transcaspicus* as a species in its own right; the name was occasionally associated with *arvalis, ilaeus*, *kermanensis*, *khorkoutensis* and *transcaspicus*. Species status of *transcaspicus* is well-supported by nucleotide sequences (Mahmoudi et al. 2017a), karyotype and peculiarities of morphology, in particular the small sperm head and large baculum (Malygin 1983). The Transcaspian vole is in a sister position against the *arvalis*+*mystacinus* species groups with TMRCA 0.238 Mya (Mahmoudi et al. 2017a); karyological data suggest close affinities between *transcaspicus* and *rossiaemeridionalis* (Meier et al. 1985). Cross-breeding trials with *arvalis* and *mystacinus* species groups yielded sterile offspring (Bikchurina et al. 2021).

Distribution (Figure 305). Range of 159,587 km^2 is in two fragments. The western fragment is in Kopet Dag and on the border between Turkmenistan (provinces of Ahal, Balkan, and Mary) and Iran (north-eastern Khorassan-e-Razavi and adjacent Golestan). The eastern fragment is in Hindu Kush (Afghanistan) with records in Baghlan, Bamian, Kabul, Laghman, Lowgar, Parwan, Takhsar, and Wardak. Transcaspian grey voles occupy humid meadows with lush grass shaded by trees in river valleys and on flooded lowlands. Such sites are sporadic and the range is fragmented at a finer scale. Lower altitudes are inhabited in Kopet Dag (usually 500–1,500 m) than in Afghanistan (2,500–2,800 m; Niethammer 1970a, Hassinger 1973, Kucheruk & Khlyap 2005).

Characteristics. A large and long-tailed grey vole (TL/H&B=0.35–0.46). Dimensions: BWt=36–67 g, H&B=115–147 mm, TL=41–61 mm, HF=18–25 mm, EL=12.3–17 mm, CbL=28.1–33.8 mm, ZgW=15.4–18.9 mm, MxT=6.9–8.7 mm. Fur is rather soft, 9.5–14 mm long (protruding hairs measure 12–16 mm). Back is rich-brown with rusty shade or dull buffy-grey; grizzled yellow. Underside is grey shaded with buffy or brown tint. Subadult voles are darker with more abundant black hairs. Tail is obscurely to distinctly bi-chromatic, greyish brown above and whitish below; annulation is not hidden under hairs and the terminal pencil is sparse (length=2–5 mm). Ears are grey and edged by short buffy hairs; paws are whitish to grey. Skull shows no peculiarities; it is moderately wide (mean ZgW/CbL=0.53–0.57) and not very ridged; interorbital crest is prominent in old animals. The septum on the posterior palatine is moderately wide and the naso-frontal suture is wide and straight. Bullae are relatively small (Figure 306). The alveolar process on the outer side of the mandibular ramus is indistinct. Molars show no peculiarities and hardly any individual variability (Figure 307); M^3 is relatively short and has 4 inner and 3 outer salient angles. M_1 has confluent dental areas of salient angles BS4 and LS5 with the anterior cap; BS3 on M_2 is prominent and closed. Baculum is like in *arvalis* but larger: length×width of proximal baculum=2.90–3.60 × 1.80–2.30 mm. Length of distal baculum is 1.20–1.70 mm (central digit) and 1.00–1.30 mm (lateral digit); central digit is on average 1.25-times longer than the lateral digit (Aksenova 1980). Sperm head is smaller than in other grey voles: length×width=6.30–7.38 × 3.15–3.60 µm (Aksenova 1978).

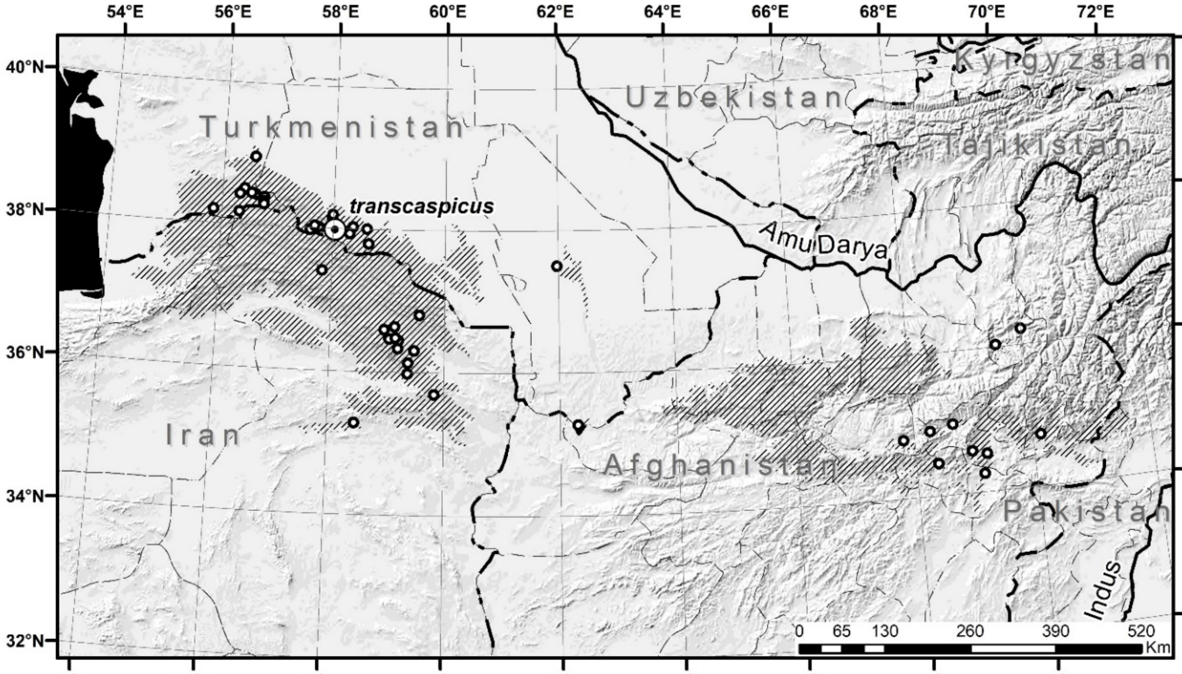
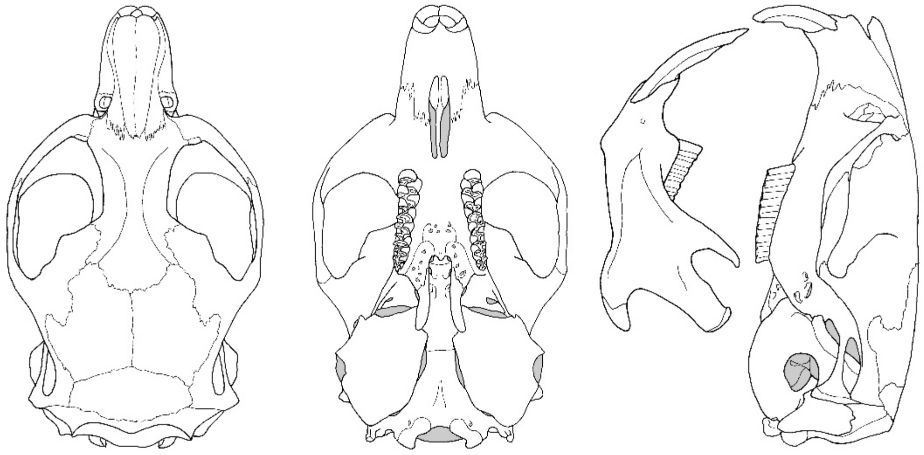
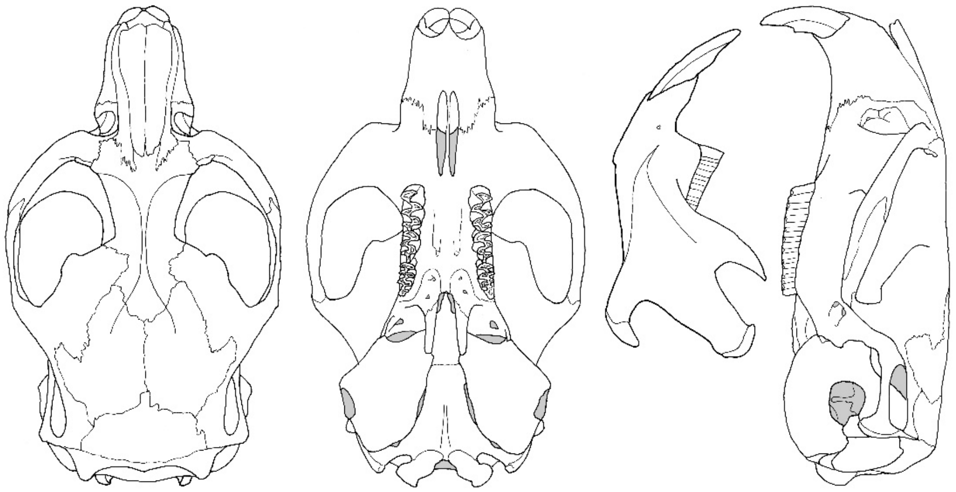


Figure 305: Distributional range of the Transcaspian grey vole *Microtus transcaspicus*.

Microtus ilaeus ilaeus



Microtus ilaeus igromovi



Microtus transcaspicus

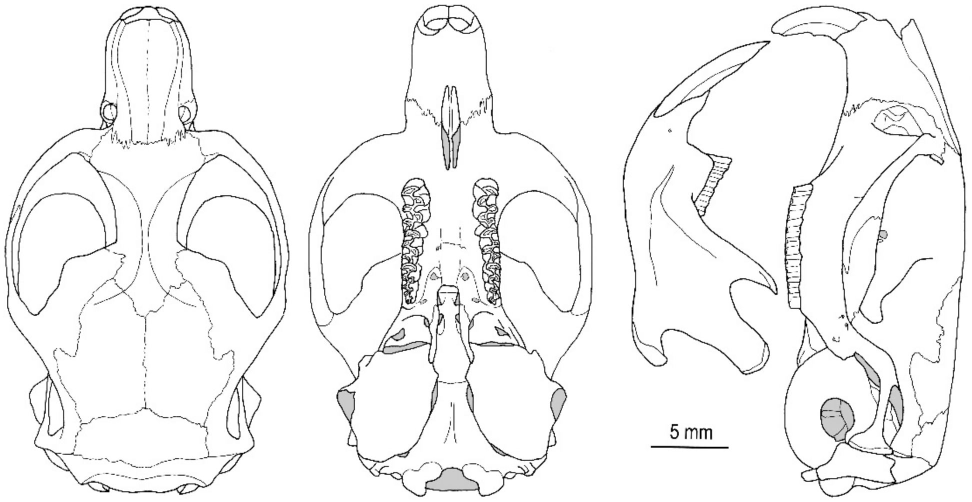


Figure 306: Skull in grey voles: top–*Microtus ilaeus ilaeus* (Arvanskyi, Bulak Keklik Too, Kyrgyzstan); middle–*M. ilaeus igromovi* (Uzbekistan); bottom–*M. transcaspicus* (western Kopet Dag, Turkmenistan).

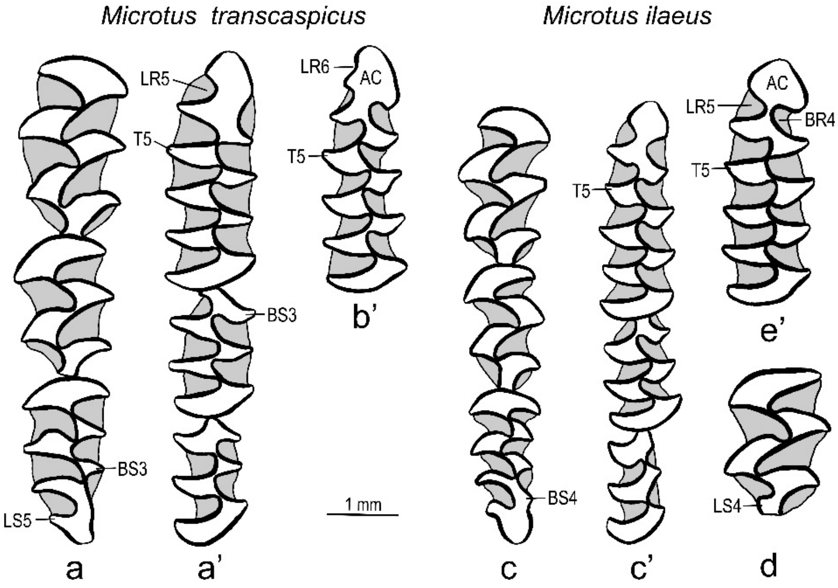


Figure 307: Molar pattern in grey voles. *Microtus transcaspicus*: upper (a) and lower row (a'–Paghman, Afghanistan); isolated M_1 (b'; Turkmenistan). *M. ilaeus*: upper (c) and lower row (c'–ssp. *ilaeus* from Tonsky, Ottuk, Kyrgyzstan); isolated M^2 (d) and M^1 (e'–ssp. *igromovi* from Uzbekistan).

Karyotype: 2n=52, NF_a=54; all chromosomes are acrocentric except for one pair of large submetacentric autosomes (Malygin 1983, Mahmoudi et al. 2014b). Sex chromosomes are large.

Variation and subspecies. Monotypic.

Subgroup *ilaeus*

Microtus ilaeus Thomas, 1912 – Kyrgyz Grey Vole

Taxonomy. Occasionally reported as *kirgisorum* Ognev; associated with *arvalis*, *obscurus* or *transcaspicus* in the past.

Mt-phylogenetic reconstruction retrieved basal position of *ilaeus* in the *arvalis* group (Mahmoudi et al. 2017a) and chromosomal evidence concurs with this (Meier et al. 1985). Time for TMRCA is estimated at 0.315 Mya (Mahmoudi et al. 2017a). Cross-breeding trials with *arvalis, transcaspicus* and *rossiaemeridionalis* yielded sterile offspring (Meier et al. 1985, Meyer et al. 1996).

Analysis of ancient DNA retrieved a sister lineage to a recent *ilaeus* among the Late Pleistocene material in Crimea and from two sites in Bulgaria, i.e. 1,000–2,000 km west of the current distribution of *ilaeus* (Baca et al. 2021). The two lineages are separated by the average *Cytb* distance of 4.9%.

Distribution (Figure 308) (area=211,000 km^2) covers Uzbekistan, very marginally Turkmenistan (Lebap) and Tajikistan (Sughd), northern Kyrgyzstan (Ysyk-Köl, Osh, Jalal-Abad, Chu, Batken), and south-eastern Kazakhstan (Kzyl-Orda, Dzhambul, Chimkent, Almaty); present also in north-western and north-central Xinjang (China). The range is in two fragments, the larger eastern and the smaller western (for details see under subspecies). Kyrgyz grey voles populate humid to marshy ground in tall-grass pastures, mountain forests, and in flooded river-valleys (Ma et al. 1987, Davydov 1988, Meyer et al. 1996, Kucheruk & Khlyap 2005) Altitudinal range is between 40–2,970 m but rarely goes above 2,700 m.

Characteristics. Large vole with a moderately long tail (TL/H&B=0.26–0.49). Because of significant interpopulational differences, external traits are detailed under subspecies. The skull is like in *transcaspicus* but the nasals are longer and the naso-frontal suture is more constricted. The braincase is longer and narrower (Figure 306); temporal ridges are prominent in adults. The alveolar process on the outer side of the mandibular ramus is indistinct. Molars (Figure 307c-e'): M^2 frequently has an additional salient lingual angle (LS4) which, however, is not fully closed; M^3 has a feeble 4th labial salient angle BS4. Distal re-entrant angles (BR4 and LR5) on M_1 are occasionally deep enough to isolate the anterior cup from dental fields T6–T7. Baculum is like in *transcaspicus* but smaller and with a more expanded base: length×width of the proximal bone=2.10–2.85 × 1.00–1.75 mm. Length of distal baculum is 0.70–1.10 mm (central digit) and 0.50–0.85 mm (lateral digit); central digit is on average 1.3–1.4-times longer than the lateral digit (nominal subspecies; Aksenova 1980). Sperm head is of average size: length×width=7.00–8.55 × 3.15–4.05 μm (Aksenova 1978).

Conventionally stained karyotype does not differ between the main fragments of the species' range: 2n=54, NF_a=72; 12 pairs of autosomes are bi-armed and 14 pairs are acrocentric (Malygin 1983, Meyer et al. 1996). Sex chromosomes are large and usually acrocentric (see below).

Variation and subspecies. We follow Meyer et al. (1996) in recognising two subspecies; hybrids between them are fertile.

Microtus ilaeus ilaeus Thomas, 1912

Microtus ilæus Thomas, 1912a:348. Type locality: "Djarkent, Semiretschensk, E. Russian Turkestan. 'On banks of River Ussek'"; type locality is in Panfilovskiy Rayon, Almaty Oblast, Kazakhstan.

Synonyms. *Microtus arvalis kirgisorum* Ognev, 1950.

Distribution. The eastern major fragment: Mountains of Central Asia between Turkestanskiy Khrebet (Ridge) in the west and Dzhungarskiy Alatau, Kermen Khrebet, and eastern Tien Shan in the east: Chatkalskiy Khrebet, Ferganskiy Khrebet, Pskemskiy Khrebet, Talas Basin, Talaskiy Alatau, Kirgizskiy Khrebet, Terskey Alatau, Kungey Alatau, Zailiyskiy Alatau, and Boro Khoro and Narat Ridges. Small isolates were reported from Eastern Tien Shan (Hejing, Xinjang; Zhan et al. 1997) and Sarykhosor (Khation, Takijistan; Davydov 1988).

Characteristics. Smaller: BWt=32–60 g, H&B=107–153 mm, TL=32–54 mm, HF=15–23 mm, EL=11–16 mm, CbL=26.0–29.6 mm, ZgW=14.4–17.2 mm, MxT=6.3–8.0 mm. Fur is moderately soft and 7–9 mm long (protruding hairs=10–13 mm); tail is modestly

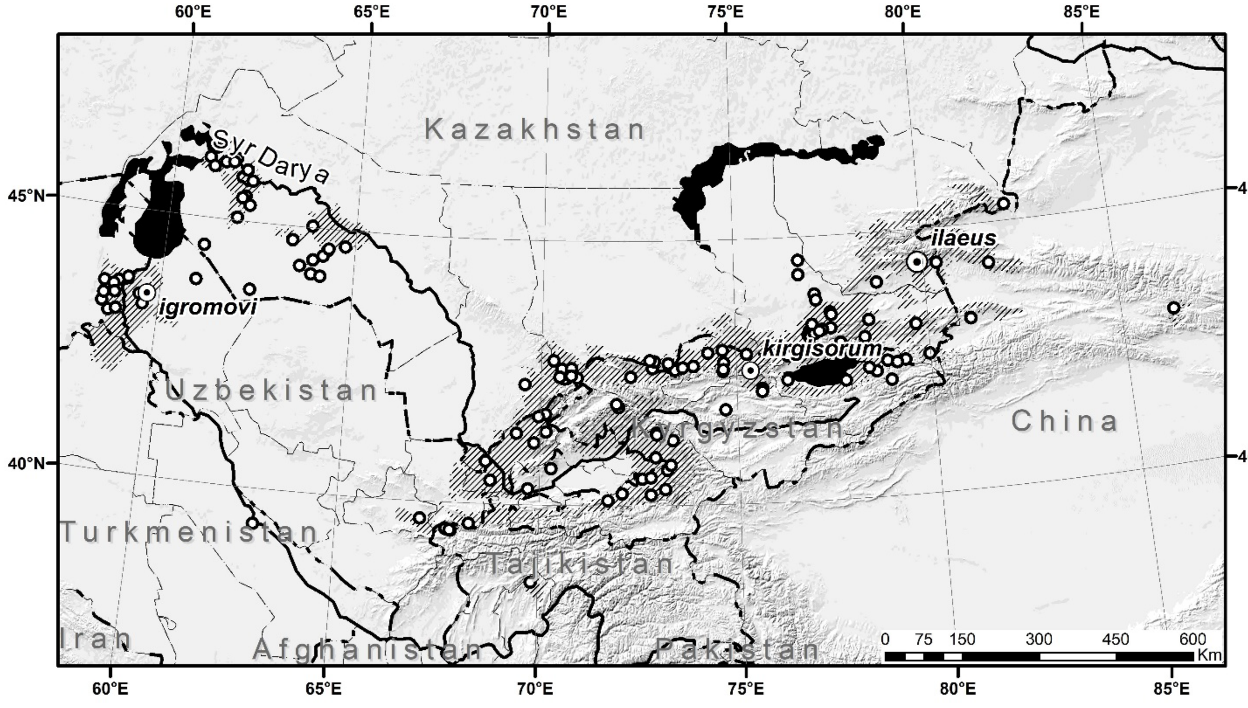


Figure 308: Distributional range of the Kyrgyz grey vole *Microtus ilaeus*.

hairy and the annulation is not concealed; terminal pencil is 3–5.5 mm long. Fur colour is brown, rarely dull and usually amply shaded buffy; dorsal side is grizzled by yellowish and blackish hair tips. Flanks are lighter (buffy or light-fawn) and the demarcation between the back and belly is obvious; belly is greyish with slate hair bases. Paws are whitish-grey to grey, tail bi-chromatic greyish-brown to blackish-brown above and grey or greyish white below. Ears are grey to dull brown. Supratemporal ridges rarely merge into interorbital crest which remains short (Figure 306). Baculum is shorter (3.0–4.0 mm; Aksenova 1980).

Microtus ilaeus igromovi Meyer & Golenishchev, 1996

Microtus ilaeus igromovi Meyer & Golenishchev, 1996 (in Meyer et al. 1996:272). Type locality: "pond Daukemir in the vicinity of a settlement Kazakhdarya, Muynakskiy rayon, Karakalpakia", Uzbekistan.

Taxonomy. Ognev (1950) classified voles from Syr-Darya in *ilaeus,* which he considered to be subspecifically distinct from his *kirgisorum*.

Distribution. Restricted to the western major fragment. The range is subdidided into two fragments along the Amu-Darya River, i.e. Karakalpakia (northern Uzbekistan) and its middle course in Turkmenistan. Further two fragments are along the Syr-Darya River; the one in its estuary and the other further upstream around Kzyl-Orda (southern Kazakhstan). Additional small isolates are scatered here and there in the area (Kucheruk & Khlyap 2005).

Characteristics. Larger: BWt=36–64 g, H&B=105–150 mm, TL=33–56 mm, HF=19–23 mm, EL=11–15 mm, CbL=28.3–32.8 mm, ZgW=15.8–18.6 mm, MxT=6.9–8.1 mm. Fur is softer and longer (8–11 mm; protruding hairs measure 12–15 mm), terminal pencil is longer (5–6.5 mm). Pelage is lighter due to ample yellowish (buffy) tint; extreme individuals are yellowish. Flanks are buffy, demarcation is either distinct or blurred; belly is whitish, clouded with slate underhair and washed buffy in some individuals. Tail is usually distinctly bi-chromatic (light brownish-grey above, light grey below). Skull is heavier and more ridged (Figure 306); interorbital crest is longer than in the nominal subspecies. Molars (M^2, M_1) tend to be more complex (Figure 307d,e'). Baculum is longer (4.0–4.3 mm; Meyer et al. 1996).

Species group *socialis* – Social voles

Taxonomy. The *socialis* species group has an identical taxonomic scope to *Sumeriomys*. The latter was established as a subgenus of *Microtus* to encompass short-tailed voles with dense, soft pelage, 5 plantar pads, a flat interorbital region and enlarged petromastoid and auditory bullae (Argyropulo 1933). The recognition of *Sumeriomys* as a subgenus has varied over time. While Ellerman (1948) openly rejected it, Migulin (1938) treated *Sumeriomys* as a genus in its own right. Many authors, particularly in the former Soviet Union, used *Summeriomys* as a subgenus as originally proposed. The majority opinion, however, classified social voles in *Microtus* without further subranking or, more rarely, in the subgenus *Microtus.* In the subgenus *Microtus*, social voles were sometimes aligned in the *socialis* species group, a view which was supported by molecular phylogenetic reconstructions (Jaarola et al. 2004, Steppan & Schenk 2017, Thanou et al. 2020) and is followed here.

Several alternative phylogenetic scenarios for social voles and their taxonomic solutions are worth mentioning although they never gained wide support. Ognev (1916, 1950) classified social voles in the Nearctic *Chilotus* Baird, 1857 (as a subgenus of *Microtus*) and Lataste (1886) placed *socialis* into *Pitymys.* Goodwin (1935) saw his *M. (socialis) gravesi* as a close relative to *Phaiomys*, while Chaline (1974) classified social voles into *Suranomys* (a subgenus of *Microtus*). Brink (1956) classified *guentheri* in *Iberomys*, together with *cabrerae* and *dentatus* (now in *Iberomys*) as well as with *asturianus* and *igmanensis* (synonyms of *M. arvalis*); this concept was accepted by Chaline & Mein (1979) and Honacki et al. (1982). Honacki et al. (l.c.) therefore classified *socialis* and *irani* into *Sumeriomys* and *guentheri* as *Iberomys.*

Although social voles are phylogenetically close to grey voles, (Malygin 2015) they differ in several external and cranial traits (Kryštufek & Vohralík 2005, Mahmoudi et al. 2017b), in sperm morphology (Aksenova 1978), and copulatory behaviour (Zorenko 2013, Rutovskaya 2019b). Hybrids between social and grey voles are sterile (Kovalskaya et al. 2014, Malygin 2015).

The number of species of social voles varied between 1 (Ognev 1950, Lay 1967, Corbet 1978, Harrison & Bates 1991) and 8 (Musser & Carleton 2005, Shenbrot & Krasnov 2005). A 3-species taxonomy (*guentheri, socialis* and *irani*) was the prevailing solution throughout the 2nd half of the twentieth century (cf. Ellerman 1948, and Musser & Carleton 1993). We recognise 8 species which are in two subgroups (Kryštufek et al. 2009, Martínková & Moravec 2012, Steppan & Schenk 2017), the *socialis* and *guentheri* subgroups. These subgroups putatively diverged 0.9 Mya (Thanou et al. 2020).

Distribution. Social voles occupy structurally simple and well-drained upland habitats with >20 cm deep soil layer and graminoid vegetation. The elevational range is from sea level up to 3,300 m a.s.l. Although their ranges lie at the very southern border of arvicoline distribution, social voles are more tolerant to low than to high temperatures and cannot withstand ambient temperatures of 40°C (Zorenko 2013).

Despite their extensive range (from 20°30'–21° eastern longitude in Libya and the western Balkans to the 91st meridian in north-western Xinjang), the majority of social vole species occur between Central Anatolia and

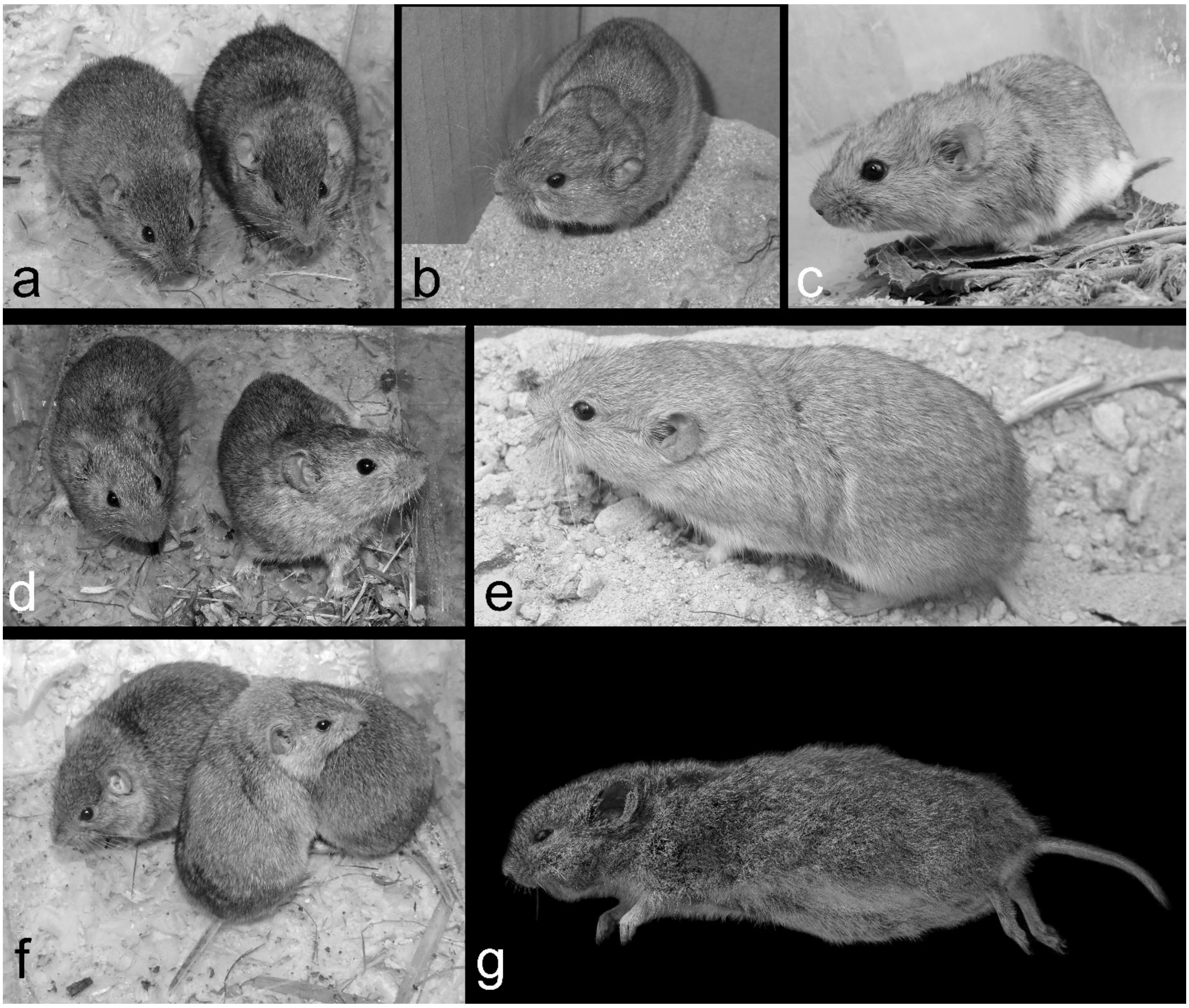


Figure 309: Representatives of social voles: a–*Microtus irani schidlovskii* from Armenia; b–*M. irani karamani* from Balkusan, Turkey; c–*M. dogramacii* from Iran; d–*M. guentheri* from Kahramanmaraş, Turkey; e–*M. anatolicus* from Yapalı köyü near Cihanbeyli, Turkey; f–*M. hartingi* from Central Anatolia; g–carcass of *M. hartingi* from Gramatikovo, Strandža Mts., Bulgaria. Photo by B. Kryštufek (a, d, f, g), Alenka Kryštufek (b, e), and Ahmad Mahmoudi (c).

the southern edge of the Turkmen Plain, i.e. with a radius of ~1,000 km. It has been argued that south-western Asia is their cradle (Kryštufek et al. 2009). The western range in south-eastern Europe was likely only recently formed (Kryštufek et al. 2018) and no social vole fossils have ever been reported west of Greece (Kowalski 2001). The only exception is the recently described *M. (Sumeriomys) bifrons* which was based on 11–20 ky old remnants in France (Jeannet & Fontana 2015). The classification of *bifrons* as a social vole requires verification. Earlier reports of *Arvicola guentheri* (Scully 1887) and *M. socialis* (Hassinger 1973) for Afghanistan are erroneous.

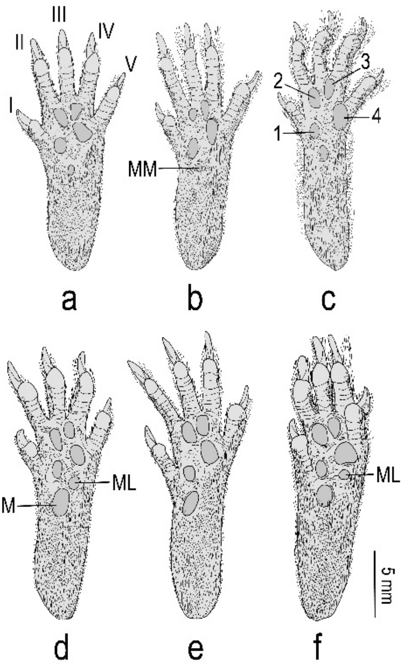


Figure 310: Left sole in social voles: a–*Microtus socialis* from Crimea, b–*M. irani* (Balkusan, Turkey); c–*M. anatolicus* (Yapalı köyü, Cihanbeyli, Turkey); d–*M. guenthetri* (Sweida, Syria); e,f–*M. hartingi* from Dobroveni near Bitola, North Macedonia (e), and Gramatikovo on the Strandža Mts., Bulgaria (f).

Characteristics (Figure 309). Small to medium-large voles with large eyes, (eye diameter in *hartingi* is 4.4–4.8 mm); the ears are covered by short hair (Figure 5) and protrude from the pelage. Tail is usually shorter than ⅓ the head and body. The majority of taxa have 5 plantar pads (Figure 310); nipples are like in the *arvalis* group. Bullae and the mastoid portion of the temporal bone are frequently swollen and may expand behind the condyles; supratemporal ridges are feeble and never merge into a sagittal crest. Molars as in the *arvalis* group with a tendency towards an additional postero-lingual salient angle LS4 on M^2 and more rarely on M^1. M^3 normally has 4 inner and 3 outer salient angles. M_1 has 5 alternating triangles and a trifoliate anterior cup. The sperm head is oval with a rounded head cap; the quotient of head length with its width as denominator is 1.8–2.4 (1.42–1.50 in the *arvalis* group); the middle piece of the sperm tail is 2.4–2.7-times longer than the head (2.8–3.2-times in the *arvalis* group; Zorenko & Golenishchev 2015).

Key to species

1a) Medial metatarsal pad is large ………….............. 2
1b) Medial metatarsal pad is tiny …………………...... 5
2a) Occurs in Africa ………………………….... *mustersi*
2b) Occurs in Europe and/or Asia ……………….. 3
3a) M^2 usually with postero-lingual salient angle LS4 (T5); M^3 with 4 labial salient angles in at least ½ of individuals ……………………………........*dogramacii*
3b) M^2 usually without postero-lingual salient angle LS4 (T5); M^3 usually with 3 labial salient angles ……………………………………………….... 4
4a) Plantar pads usually 5; base of baculum is rounded, occasionally having a medial notch ………..... *hartingi*
4b) Plantar pads usually 6; bacular base is triangular with a prominent posteriorly directed protuberance ……………………………………….......*guentheri*
5a) Upper incisors proodont; nasals short; praelambdoid fenestrae not entirely filled with bony tissue; bullae short and the mastoid portion not particularly swollen; alveolar process prominent; $2n=60$, $NF_a=58$ ………………........................ *irani*
5a) Upper incisors orthodont; nasals of normal length; praelambdoid fenestrae are filled with bony tissue; bullae enlarged and the mastoid portion swollen; alveolar process feeble; karyotype different from above …………………... 6
6a) Incisive foramina shorter than MxT; $2n=NF_a=60$ ……………….. *anatolicus*
6b) Incisive foramina longer than MxT; $2n=62$ …………………………...................................... 7
7a) Plantar pads usually 6; distal baculum: length of central digit <110% of the lateral digit; interorbital constriction >4.0 mm; postero-lingual salient angle LS4 is present in a significant proportion of M^1 and in the majority of M^2 ……………….……….. *paradoxus*

7a) Plantar pads usually 5; distal baculum: length of central digit >120% of the lateral digit; interorbital constriction <4.0 mm; postero-lingual salient angle LS4 is normally absent on $M^{1–2}$ .... *socialis*

Subgroup *socialis*

Medial metatarsal pad is tiny and markedly smaller than the remaining tubercles; 2n=60–62. The subgroup occupies the eastern portion of the range from Central Anatolia to Xinjiang. Basal dichotomy (*socialis*+*anatolicus* vs *irani*+*paradoxus*) dates 0.74 Mya and the recent species diverged 0.61–0.64 Mya (Thanou et al. 2020).

Microtus socialis (Pallas, 1773) – Common Social Vole

Taxonomy. Molecular evidence placed *socialis* in a sister position with respect to *anatolicus*. The two species are allopatric and clearly differ in morphology and diploid number of chromosomes (Kryštufek & Vohralík 2005); their dichotomy is dated at 0.64 Mya (Thanou et al. 2020).

Distribution (Figure 311). The range is the largest in the genus (area=1,779,685 km^2) and extends from Crimea and southern Ukraine (provinces of Dniepropetrovsk, Donetsk, Kherson, Lugansk, and Zaporizhzhya) across the cis-Caucasian steppes in southern Russia (Rostov, Stavropol', Kalmykia, Kabardino-Balkariya, North Ossetia, Dagestan, Chechnya, Volgograd, Astrakhan', and Saratov) into Kazakhstan (West Kazakhstan, Atyrau, Aktyubinsk, Kzyl-Orda, Quaraghandy, Chimkent, Zhambyi, Alma-Ata, and East Kahakhstan) and through northern Tajikistan (Sught) and northern Kyrgyzstan (Bishkek) reaching north-western Xinjiang (China). Populations in south-western Asia, which are nearly perfectly isolated from the main range by the Caucasian ridge, occupy eastern and central Georgia, southern Armenia, Azerbaijan, eastern Turkey (Bayburt, Kırşehir, Çorum, Erzurum, Gaziantep, Sivas, Van) and north-western Iran (Ardabil, Azarbayjan-e-Gharbi, Gilan, Kordestan, Mazandaran, Tehran, Zandjan, and Zanjan). Common social voles occupy open grassy-herbaceous habitats on chernozome, clay, sands or saline soils, from below sea level (–27 m in the Caspian area) up to 3,300 m a.s.l. These voles are regionally abundant; under xeric conditions they are sporadic and restricted to moist sites. Over the last century deforestation and irrigation enabled local range expansions of up to 30–40 km (Vereshchagin 1959, Tembotov 1972, Shlyakhtin et al. 2009, Bukreeva & Lidzhi-Garyaeva 2018).

Description. The smallest social vole with a short tail (TL/H&B=0.17–0.36). Ears are small but not concealed in the fur. There are 5 (rarely 6) palmar pads (Figure 310a); in Dagestan, 9% of voles have 6 pads on both soles and a further 15.4% show asymmetric counts of 5 and 6 pads (Golenishchev et al. 2002). Hair is thick and moderately long (7.5–9 mm; the longer dark-tipped hairs measure 9–10 mm); hairs on the tail do not usually conceal the annulation; the terminal pencil is short (length=1.5–3.5 mm). Pelage colouration varies (see under subspecies); back is usually greyish-buff to greyish-brown and speckled by dark hair tips; the flanks are frequently clearly buff and lack the grizzled effect. The underside is usually grey and hairs frequently have white or cream tips; buffy tint is rare. The demarcation line on the flanks varies from obscure to distinct. The tail is usually bi-chromatic, dark brown above and cream below; its dorsal surface has a middle dusky stripe in some populations. Ears are brownish-grey and the post-auricular hairs are frequently buff; feet are light grey to cream and may have a dark mid-tarsal stripe. The skull is small and delicate (Figure 312) with moderately expanded zygomatic arches (ZgW/CbL=0.52–0.61) and a flat interorbital region; the braincase is large and deep (height across bullae/CbL=0.34–0.41). Bullae are swollen (length of bullae/CbL=0.33–0.39) and the mastoid portion of the temporal is inflated; in populations with pronouncedly swollen bullae, the mastoid chamber extends till the level of the occipital condyles or even beyond. The medial process of the posterior hard palate is either sharply defined or low and ill-pronounced. Incisive foramina are long. The bulge of the alveolar process on the outer side of the mandibular ramus is indistinct. Molars show no peculiarities; M^1–M^2 usually lack the postero-lingual salient angle LS4; M^3 has 4 inner and 3 (rarely 4) outer

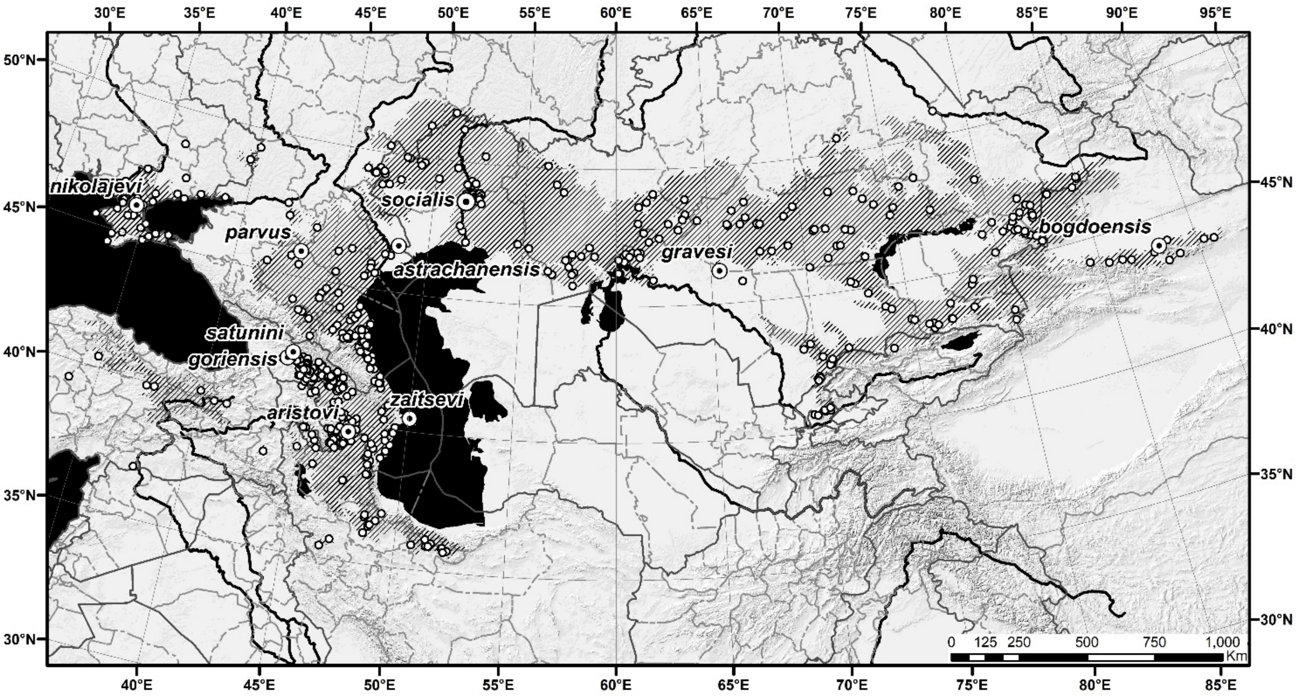


Figure 311: Distributional range of the common social vole *Microtus socialis*.

salient angles (Figure 313). Average dimensions ($\bar{x}\pm SD$; length×width) of glans penis are between 3.7±0.07 × 2.6±0.06 mm (ssp. *nikolajevi*) and 4.1±0.04 × 2.6±0.09 mm (ssp. *parvus*; Zorenko 2013). Proximal baculum is 2.05–3.15 mm long and 1.05–1.70 mm wide; length of distal digits is 1.00–1.60 mm and 0.75–1.25 mm for the central and the lateral digits, respectively (Golenishchev et al. 2002). The sperm head is 6.2–7.4 µm long and 4.3–6.0µm wide (Zorenko 2013); size varies between subspecies but width-to-length ratio remains constant (length/width≈1.40; Zorenko & Golenishchev 2015). Karyotype: 2n=62, NF_a=60; all chromosomes are acrocentric and no variation was reported among subspecies (Zima & Král 1984, Zima et al. 2013, Golenishchev et al. 2002).

Variation and subspecies. It is generally agreed that *M. socialis* is a polytypic species and 11 subspecies were listed in the most recent lists (Shenbrot & Krasnov 2005, Pardiñas et al. 2017). We have reduced this number to 8 subspecies by synonymising *hyrcania* with *transcaspicus*, *astrachanensis* with the nominal subspecies, and *bateae* with *irani*; the status of *goriensis* requires clarification. Our review mainly follows Ognev (1950) and Golenishchev et al. (2002); the latter placed heavy emphasis on the morphology of the baculum. Differences between subspecies are average and the pattern of geographic variation is poorly known. Zorenko et al. (1997) suggested the status of species in its own right for each of the 4 subspecies (*socialis, nikolajevi, satunini, parvus*).

Microtus socialis socialis (Pallas, 1773)

Mus socialis Pallas, 1773:705. Type locality: "locis herbidioribus deserti ad Iaȉkum"; restricted to the "lowlands of the Ural river" (Ognev 1924:36).

Synonyms. *[Mus] aſtrchanenſis* [*astrchanensis*] Erxleben, 1777.

Distribution. Southern Russia (Kalmykia and east of the Volga River), and western Kazakhstan; the eastern border with *gravesi* not resolved.

Characteristics. A medium-sized and short-tailed (TL/H&B=0.17–0.24) subspecies. Dimensions: H&B=86–115 mm, TL=18–26 mm, HF=15–17 mm, EL=8–10 mm, CbL=24.0–26.8 mm, ZgW=13.1–15.5 mm, MxT=5.7–6.8 mm (Sludskiy et al. 1978). Dorsal pelage is buffy-brown to tawny, flanks are pinkish-buff; the tail is monochromatic or indistinctly bi-chromatic. Zygomatic arches widely bowed (ZgW/CbL~0.58); bullae are of normal size. Postero-lingual salient angle LS4 on M^2 is only rarely present.

Microtus socialis parvus Satunin, 1901

Microtus parvus Satunin, 1901b:46, 117. Type locality: "a steppe near the Village of Divnoe [Diwnoje on p.117], not far from the River Kalaus", Apanasenkovsky District, Stavropol Krai, Russian Federation.

Taxonomy. Kuznetzov (1944) kept *parvus* in the synonymy of the nominal subspecies. Earlier authors (Migulin 1938, Zubko 1940) applied the name *parvus* to Ukrainian social voles which are now classified as *nikolajevi* (Gromov et al. 1963).

Distribution. Steppes in southern Russia between Kalmykia, the Don River and the Caucasus; the majority of the range is in Stavropol' Krai and Dagestan.

Characteristics. Size as in the nominal subspecies but pelage distinctly buffy; tail is on average longer (TL/H&B=0.19–0.36), and skull is narrower (ZgW/CbL=0.52–0.56); bullae are swollen. Dimensions: H&B=80–118 mm, TL=17–31 mm, HF=13.4–18 mm, EL=7–12.8 mm, CbL=23.0–26.7 mm, ZgW=12.3–15.4 mm, MxT=5.4–7.0 mm. Dorsal pelage is buffy-brown with grey tint and flanks are lighter; winter fur is greyer and duskier (Ognev 1950). Distal baculum: the lateral digits shorter relative to the central digit accounting for ~70% of its length (~84%

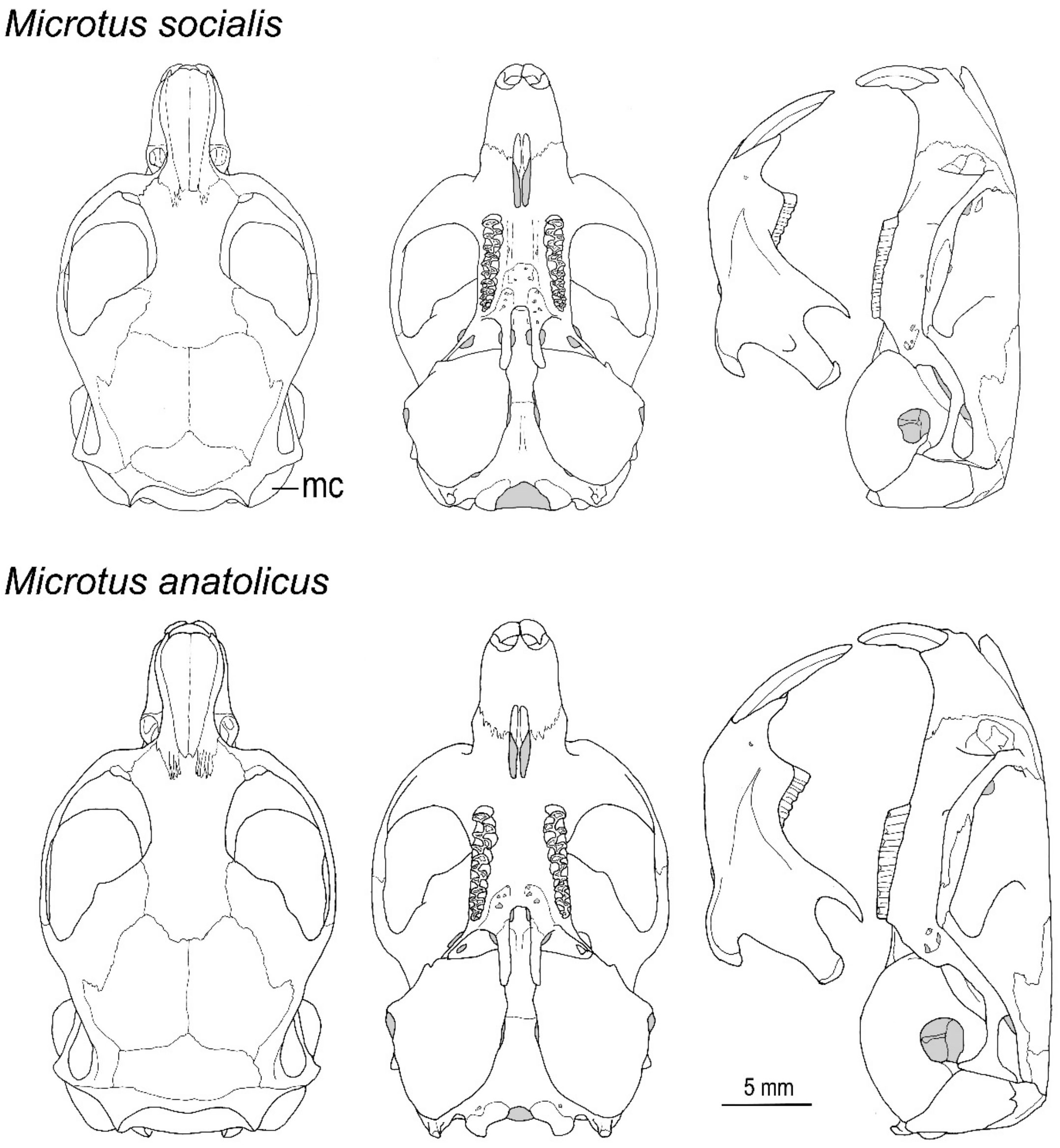


Figure 312: Skull in social voles: top–*Microtus socialis* (Dagestan, Russian Federation); bottom–*M. anatolicus* (Yapalı köyü near Konya, Turkey).

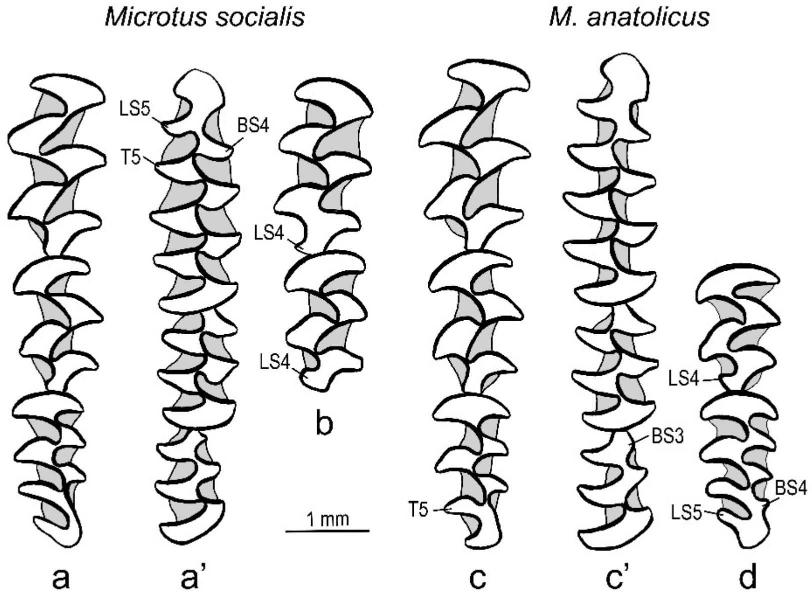


Figure 313: Molar pattern in social voles. *Microtus socialis*: upper (a) and lower row (a'–Rostov na Donu, Russian Federation); isolated $M^{1–2}$ (b–ssp. *zaitsevi*; near Baku, Azerbaijan). *M. anatolicus* from Yapalı köyü near Konya, Turkey: upper (c) and lower row (c'); isolated $M^{2–3}$ (d).

in the nominotypical subspecies; Golenishchev et al. 2002). Postero-lingual salient angle LSA4 is only rarely present on M^2; M^3 normally has 3 outer salient angles.

Microtus socialis satunini (Ognev, 1924)

Ch[ilotis] so[cialis] Satunini Ognev, 1924:37. Type locality: "c[ity] of Tiflis [Tbilisi]", Georgia.

Synonyms. *Microtus (Microtus) colchicus* Argyropulo, 1932 [preoccupied by *rubelianus colchicus* Shidlovskiy, 1919 (=*Microtus majori*)]; *M[icrotus] (Sumeriomys) schidlovskii goriensis* Argyropulo, 1935 [replacement name for *colchicus* Argyropulo]; *[Microtus socialis] binominatus* Ellerman, 1941 [substitute name for *satunini*, Ognev, which Ellerman regarded as preoccupied by "*Microtus nivalis satunini*, Shidlovskiy" (member of *Chionomys*)].

Taxonomy. The topotypes of *goriensis* display identical karyotype to *socialis* (Golenishchev et al. 2002), hence the two names are usually synonymised (Shenbrot & Krasnov 2005, Zorenko 2013, Pardiñas et al. 2017). The type of *colchicus* Argyropulo, however, shows all the essential characteristics of *irani* (proodont incisors plus a short bullae and nasals); cf. Figs. 1 & 2 in Argyropulo (1932:269–270). Until such time as new evidence emerges, we tentatively retain *colchicus* and *goriensis* in *socialis*.

Distribution. South of the Caucasus in eastern Georgia and north-western Azerbaijan; putatively also eastern Turkey.

Characteristics. A large subspecies with broadly expanded zygomatic arches (ZgW/CbL~0.59) and swollen bullae. Dimensions: BWt=22–24 g, H&B=100–122 mm, TL=24–31 mm, HF=15.9–17.9 mm, EL=8–9.5 mm, CbL=25.2–27.1 mm, ZgW=15.2–16.3 mm, MxT=6.0–7.1 mm. Dorsal side is tawny to snuff-brown with ample buffy tint on shoulders, head and rump; tail is bi-chromatic, light-grey above, whitish below. Postero-lingual salient angle LS4 is only rarely present on M^2; M^3 with 4 outer salient angles in ~½ of individuals (Golenishchev et al. 2002).

Microtus socialis gravesi Goodwin, 1934

Microtus gravesi Goodwin, 1934:2. Type locality: "Tuz Balak [Tasbalak], altitude 600 feet [185 m], 150 miles [240 km] north of Kizil Orda (Perovsk), Kazakstan, Central Asia". Tasbalak [Rock Sping] is ~220km north of Kzylorda [Qyzylorda], Qaraganda oblast, Kazakstan.

Distribution. Central and eastern Kazakhstan, northern Kyrgyzstan, north-western Tajikistan, Xinjiang (Tarbagatai Mts.).

Characteristics. A small and light-coloured vole with a wide skull (ZgW/CbL~0.61); bullae are swollen. Dimensions: H&B=80–110 mm, TL=20–26 mm, HF=14–18 mm, EL=8–11 mm, CbL=23.1–26.1 mm, ZgW=13.0–15.5 mm, MxT=5.6–6.6 mm. Dorsal pelage is buffy-grey and the auricular region is buffy; flanks are buffy and clearly demarcated against a light grey underside. Ears are brownish-grey or light grey; paws are buffy-white; tail is indistinctly bi-coloured (greyish-brown above, light grey below) or monochromatic. Baculum as in the nominal subspecies. Postero-lingual salient angle LS4 is only rarely present on M^2; M^3 normally has 3 outer salient angles.

Microtus socialis nikolajevi Ognev, 1950

Microtus (Chilotus) socialis nikolajevi Ognev, 1950:387. Type locality: "Island Kuyuk-Tuk in Sivash [lagoons]", west coast of the Sea of Azov, Crimea.

Distribution. Localities are scattered in southern Ukraine between the Dnieper and Don Rivers; north to Lugansk and Dnepropetrivsk and as far south as the Sea of Azovsk; widespread in Crimea.

Characteristics. The smallest subspecies with a moderately long tail (TL/H&B=0.19–0.30). Dimensions: H&B=83–109 mm, TL=17–29 mm, HF=14–17.5 mm, EL=7–10 mm, CbL=22.2–25.9 mm, ZgW=13.0–15.0 mm, MxT=5.3–6.5 mm. Fur is rusty-brown, the demarcation against the underside is distinct; head is more yellowish and cheeks are clear buff. Light-grey belly is clearly demarcated from buffy flanks. The proximal baculum is on average longer than in other subspecies (length up to 3.15 mm; Aksenova 1983). Zygomatic arches widely bowed (ZgW/CbL=0.58–0.62); bullae not swollen. Postero-lingual salient angle LS4 is only rarely present on M^2; M^3 normally has 3 outer salient angles.

Microtus socialis bogdoensis Wang & Ma, 1981

Microtus socialis bogdoensis Wang & Ma, 1982:112. Type locality: "Bogdo [Bogda] mountain of Fukang County, Xinjiang", China.

Taxonomy. Lunde (2008) lists only *gravesi* for China.

Distribution. Endemic to Eastern Tien Shan (northern Xinjiang, China).

Characteristics. A large and long-tailed (TL/H&B~0.30) subspecies; bullae moderately swollen. Dimensions: BWt=24–53 g, H&B=81–120 mm, TL=25–32 mm, HF=13–19 mm, EL=6–13 mm, CbL=23.4–28.0 mm, ZgW=13.8–16.2 mm, MxT=5.6–6.6 mm (Ma et al. 1987).

Microtus socialis aristovi Golenishchev, 2002

Microtus socialis aristovi Golenishchev, 2002 (in Golenishchev et al. 2002:53). Type locality: "Vicinity of Veisalli, Fizuli District, Azerbaijan."

Distribution. Nakhichevan (south-western Azerbaijan) and eastern Armenia; likely also north-western Iran (western Ardabil, Azarbayjan-e-Gharbi, Azarbayjan-e-Sharqi, Kordestan, Mazandaran, Tehran and Zanjan).

Characteristics. A dark subspecies with a long hind foot and moderately long tail (TL/H&B~0.24); bullae are swollen. M^2 with a low incidence of postero-lingual salient angle LSA4. Proximal baculum is thick and wide (greatest width=1.20–1.70 mm; Golenishchev et al. 2002). Dimensions: BWt=38.5–46.5 g, H&B=106–117 mm, TL=27 mm, HF=18–19 mm, EL=11 mm, CbL=23.1–26.5 mm, ZgW=13.6–15.6 mm, MxT=5.1–5.9 mm.

Microtus socialis zaitsevi Golenishchev, 2002

Microtus socialis zaitsevi Golenishchev, 2002 (in Golenishchev et al. 2002:54). Type locality: "Vicinity of Baku City (airport), Azerbaijan."

Distribution. Eastern Azerbaijan; likely also north-western Iran (eastern Ardabil and Gilan).

Characteristics. Lighter than *aristovi* (back is light greyish-buff); tail is monochromatic and moderately long (TL/H&B=0.19–0.33). Bullae are swollen; zygomatic arches less expanded (ZgW/CbL=0.55–0.59) than in *aristovi* (=0.57–0.63). Proximal baculum is slim and narrow (greatest width=1.15–1.25 mm; Golenishchev et al. 2002). M^1–M^2 usually with postero-lingual salient angle LS4 (Figure 313b); dental field is closed in part of the population. Dimensions: BWt=23–35 g, H&B=89–115 mm, TL=20–29 mm, HF=13–16.5 mm, EL=7–10 mm, CbL=24.4–27.8 mm, ZgW=13.9–16.5 mm, MxT=5.6–6.9 mm.

Microtus anatolicus Kryštufek & Kefelioğlu, 2001 – Anatolian Social Vole

Microtus anatolicus Kryštufek & Kefelioğlu, 2001:8. Not "*M. anatolicus* Kefelioglu et Krystufek, 2001" (Golenishchev & Abramson 2011:117). Type locality: "Turkey, Konya, Cihanbeyli, Yapalı köyü."

Taxonomy. Anatolian social vole was first reported as "*Microtus 'socialis'* 2n=60" (Kefelioğlu & Kryštufek 1999) and described shortly afterwards as a new species. Pavlinov (2003, 2006) synonimised *anatolicus* with *irani*, but phylogenetic analyses confirmed its status as a species in its own right (Kryštufek et al. 2009). It is in a sister position with respect to *socialis* (Thanou et al. 2020).

Distribution (Figure 314) Known with certainty from two localities in Aksaray Ovası (between Konya and Kayseri), the driest part of Central Anatolia. Further records from the Taurus Mts. (Yavuz et al. 2009, 2011) have a karyotype resembling *irani* and are treated as such here. Voles occupy dry alkaline soil sparsely

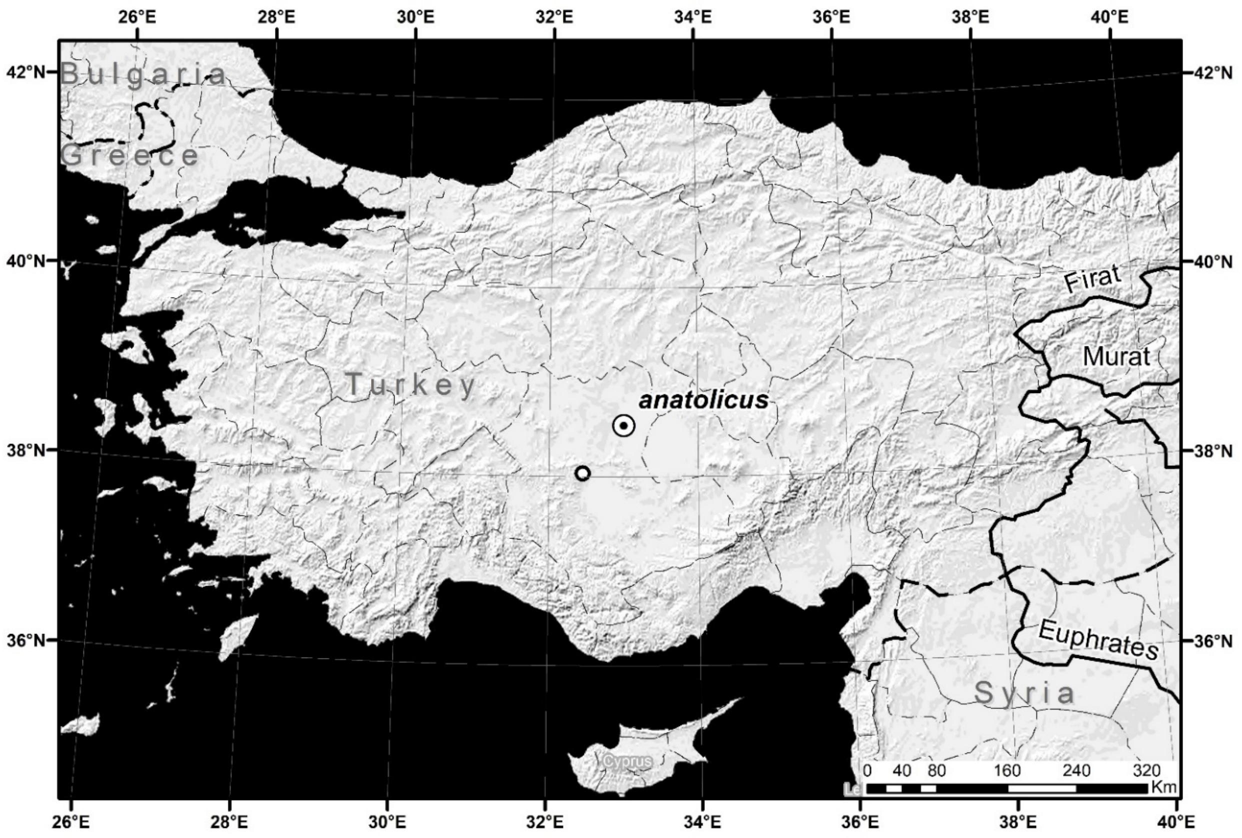


Figure 314: Distributional range of the Anatolian social vole *Microtus anatolicus*.

covered by halophytes and rushes; they concentrate in humid depressions with dense vegetation (Kryštufek & Vohralík 2005).

Description (Figure 309e). Moderately large social vole with a short tail (TL/H&B=0.23–0.28). Dimensions: BWt=23.5–53 g, H&B=105–125 mm, TL=21–34 mm, HF=16.6–23.0 mm, EL=9–11 mm, CbL=26.0–29.0 mm, ZgW=14.5–17.7 mm, MxT=6.0–7.0 mm (Kryštufek & Vohralík 2005). Fur is dense, 6–9 mm long (long protruding hairs measure 9–11.5 mm). The caudal annulation is hidden under the hair and the terminal pencil measures 2–4 mm. Dorsal pelage is buffy-cream or buffy-grey and grizzled with black tips of longer hairs. The auricular region is sometimes yellow while cheeks are either grey or buffy. Flanks are buffy or buffy-grey and the demarcation towards the underside is obscure; belly is white or creamy and heavily washed by slate underhair. The tail is greyish all-around yet obscurely bi-chromatic, darker above and lighter below. Feet are light grey and ears are grey. The skull is rather deep (height of rostrum behind M^3/CbL=0.27–0-29) with moderately expanded zygomatic arches (ZgW/CbL=0.55–0.61), a wide braincase and large bullae (length of bullae/CbL=0.34–38). Mastoid portion is enlarged and the praelambdoid fenestrae are largely filled with the bony tissue of the supramental triangle. The medial process of the posterior hard palate is ill-defined and imperfectly separates the two lateral pits. Incisive foramens are short (shorter than the upper molar-row). The bulge of the alveolar process on the outer side of the mandibular ramus is ill-defined. Molars show no peculiarities (Figure 313c,d). The postero-lingual salient angle LS4 on M^2 is present in 15% of skulls but its dental field is never closed. M^3 has 3 re-entrant angles on either side; additional posterior re-entrant angles, when developed at all, are shallow; the triangle T4 is normally part of the heel. M_1 has 4 outer and 5 inner re-entrant angles; the antero-labial salient angle BS4 of M_3 is rudimentary or entirely absent. Karyotype: $2n=NF_a=60$; X is acrocentric and Y is subtelocentric (Kefelioğlu & Kryštufek 1999, Arslan et al. 2016).

Variation and subspecies. Monotypic.

Microtus irani Thomas, 1921 – Iranian Social Vole

Taxonomy. Taxonomic scope of *irani* was confused for some time (for early definitions see Kock et al. 1972, Morlok 1978, and Kock & Nader 1983) and the name was a catch-all with 6 different diploid counts (2n=46, 48, 54, 60, 62, 64; in part reviewed in Zima et al. 2013) and several current species (*paradoxus, dogramacii*, and *mustersi*). Taxonomic scope began to be disentangled when the molecular makeup of topotypical *irani* became known (Kryštufek et al. 2009) and when the close relationships between *irani* and *schidlovskii* had been demonstrated (Zorenko et al. 2014); for the taxonomic history of *schidlovskii* see under subspecies. Here we follow the definition of *irani* from Pardiñas et al. (2017) with the addition of *bateae*. *M. irani* is a sister species to *paradoxus* and the two diverged 0.61 Mya (Thanou et al. 2020).

Distribution (Figure 315). Western part of the Zagros Mts. in north-western Iran (Kordestan and Chahar Mahall va Bakhtiari), as far south as Shiraz (Fars). The range likely incorporates the adjacent mountains of Iraq where *irani* was reported by Mahdi & Georg (1969) and Kadhim et al. (1977); these records need verification. Further north the vole is present in eastern Turkey (Van, Hakkari, Kars, Mardin, Bitlis and Niğde), western Armenia (Provinces of Aragatsoni, Ararat, Shirak, Lori), and reaches southern Georgia in Kvema-Kartli and Samtskhe-Javakheti. Iranian social voles are present further west along the Mediterranean coast in the central Taurus (Toros) Mts. in southern Turkey (Antalya and Konya) and along the Levant coast in Syria (Hamad and Idlib), Lebanon (Mont-Liban and Liban-Nord) and likely northern Israel. The gap between the Tigris and the Levant coast is likely a sampling artefact. The distribution of *irani* is rather poorly documented and some records still lack secure taxonomic identification. The Iranian social vole is largely tied to meadows, pastures, gardens and similar small-scale cultivations in the mountains. Distributional range is estimated at 263,425 km^2 and the species was found at altitudes between 200–2,700 m.

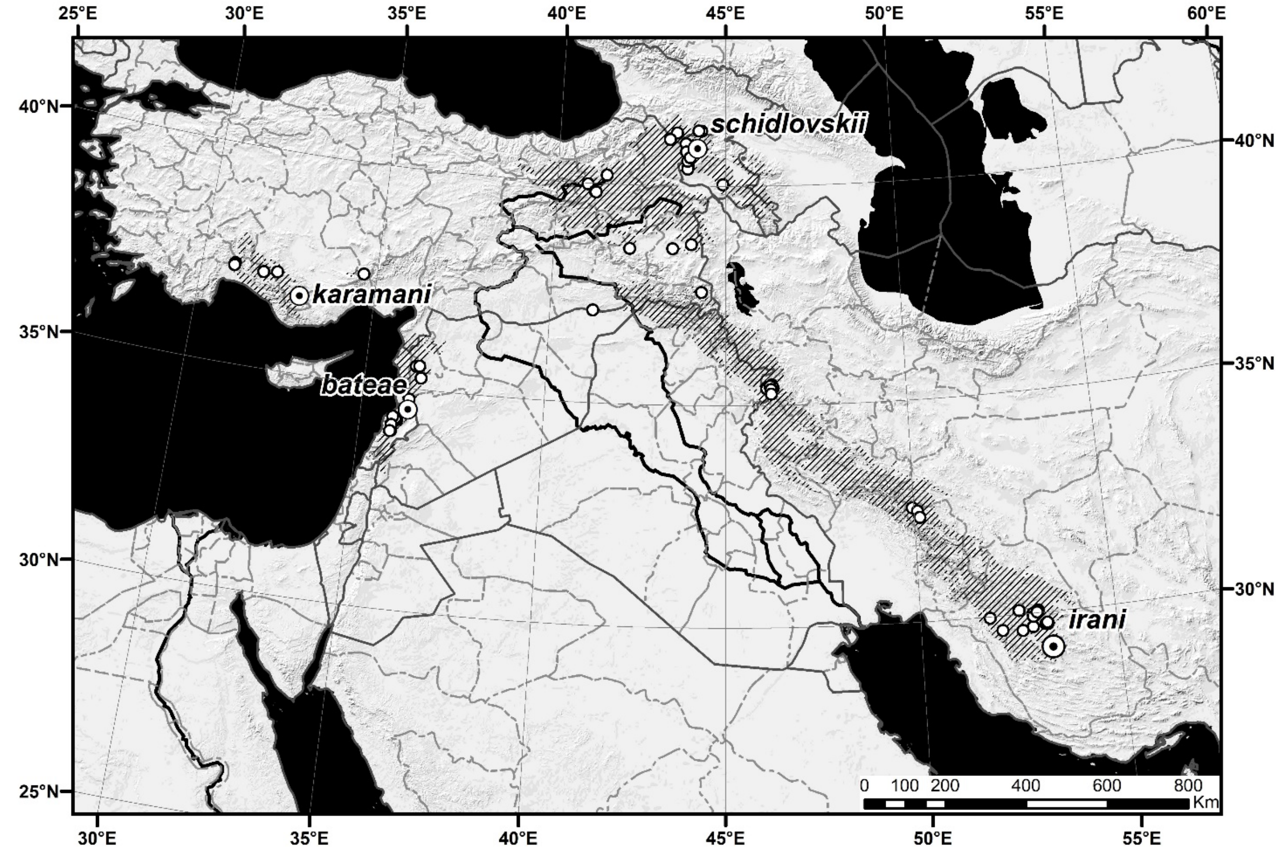


Figure 315: Distributional range of the Iranian social vole *Microtus irani*.

Characteristics (Figure 309a,b). A medium-sized and short-tailed vole with 5 plantar pads (Figure 310b). Fur is soft to silky, length of hairs is 8–10 mm and longer dark-tipped hairs measure 9.5–13 mm; terminal pencil is short (length=2–3 mm). Dorsal fur varies between pale sandy-buff to brown and is speckled by dark hair tips; flanks are usually buff and the belly is light grey, frequently tinted cream or buff. Tail is indistinctly bi-chromatic, buff-grey above and dirt white below; feet are whitish-cream to light-grey; ears are grey. Cranially, *irani* is the most distinct social vole in Iran (Mahmoudi et al. 2017b) but the skull differs among subspecies (see below). Bullae are of moderate size (bullae length/CbL=0.27–0.35) (Figure 316); the medial spine of the posterior palate is low and ill-defined. The alveolar process is swollen on the lingual side of the mandibular ramus. Molars (Figure 317a-b'): M^2 in ~10% of individuals with an additional postero-lingual salient angle LS4 (dentine field occasionally closed); a similar although less protuberant salient angle is occasionally present on M^1. M^3 is complex with 4–5 lingual and 3–4 buccal salient angles. M_1 as in other social voles; T6 is rarely closed; salient angle BS3 on M_3 is variable, either small or large but only rarely entirely absent.

Glans penis is on average 4.4 ±0.21 mm long and 2.8 ±0.06 mm wide; the proximal baculum is 2.27 mm long and 1.8 mm wide across the base; length of distal baculum is 1.05 mm and 0.95 mm for central and lateral digits, respectively. The sperm head in *schidlovskii* is 6.0–7.4 µm long and 4.8–5.0 µm wide (Zorenko 2013). Karyotype: 2n=60, NF_a=58; both heterosomes are acrocentric (Kryštufek et al. 2010, Arslan & Zima 2014, Arslan et al. 2016). Other diploid counts (2n=46, 48, 54, 62, 64) reported for *irani* are either erroneous (2n=64) or result from taxonomic confusion with *dogramacii* (2n=46, 48, 54) and *socialis* (2n=62).

Variation and subspecies. *M. irani* is genetically more variable than any other social vole. Pardiñas et al. (2017) recognised 3 subspecies; following phylogenetic results in Mahmoudi et al. (2014c) we list 4 subspecies; the lineage from Iranian Kordestan has yet to be named.

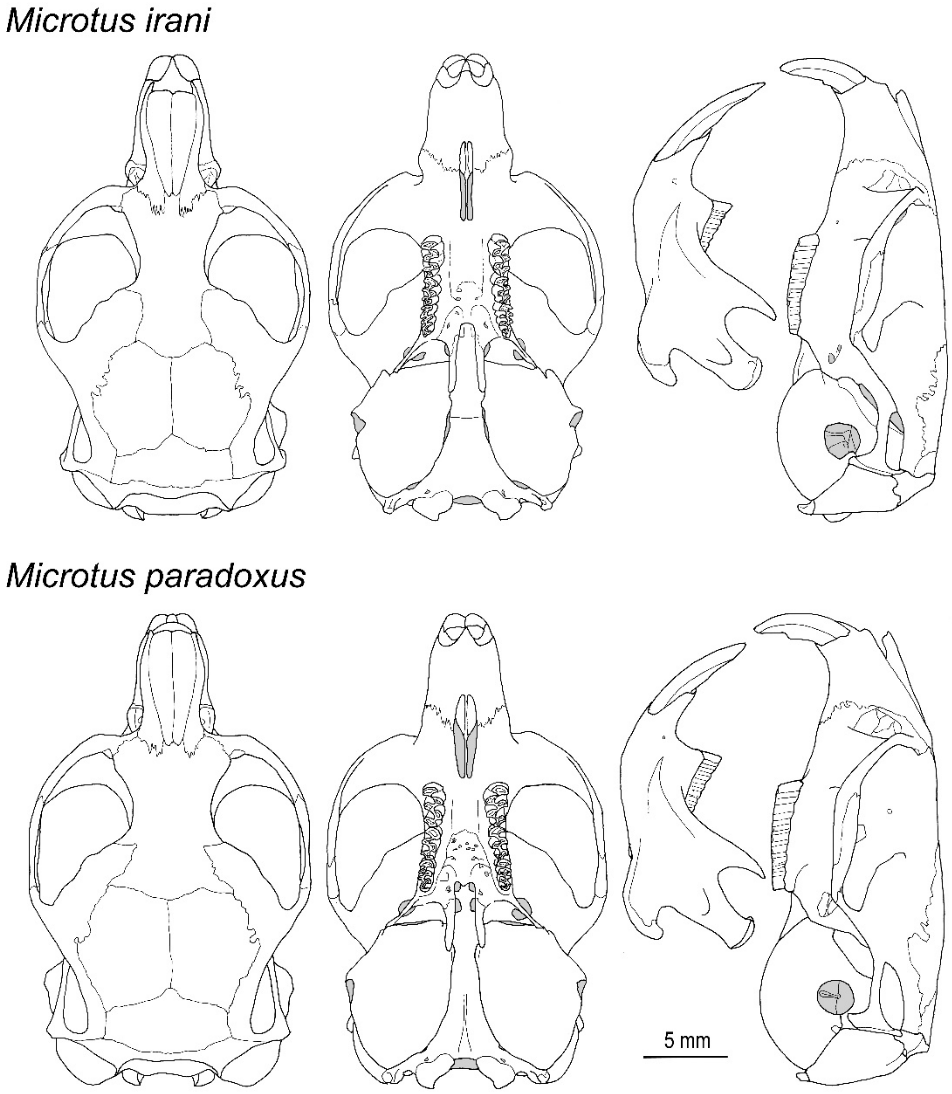


Figure 316: Skull in social voles: top–*Microtus irani* (Shiraz, Iran); bottom–*M. paradoxus* (North Khorasan Province, Iran).

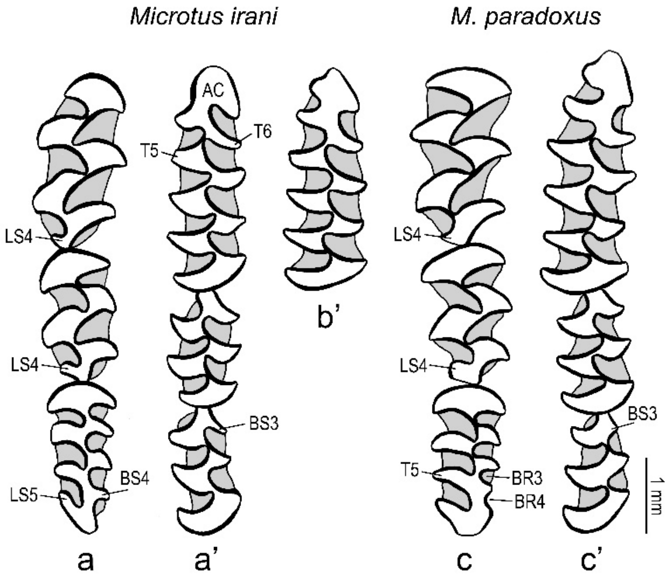


Figure 317: Molar pattern in social voles. *Microtus irani*: upper (a) and lower row (a'; Shiraz, Iran) and isolated M$_1$ (b'–Balkusan, south of Konya, Turkey). *M. paradoxus* from North Khorasan Province, Iran: upper (c) and lower row (c').

Microtus irani irani Thomas, 1921

Microtus irani Thomas, 1921 (in Cheesman 1921:581). Type locality: "Bagh-i-Rezi, Shiraz, Alt[itude] 5,200' [1,585 m]", Iran.

Distribution. Known with certainty from Fars (cf. Demirtaş & Gürler 2018).

Characteristics. A moderately large subspecies with a proportionally long tail (TL/H&B=0.20–0.35). Dimensions: H&B=92–112 mm, TL=21–37 mm, HF=16–19 mm, EL=10–12 mm, CbL=24.6–30.1 mm, ZgW=14.6–18.1 mm, MxT=5.2–7.0 mm. Dorsal pelage is pale sandy-buff with rusty tint; flanks are buff. Skull has broadly expanded zygomatic arches (ZgW/CbL=0.57–0.63); nasals are short and upper incisors are proodont (Figure 318).

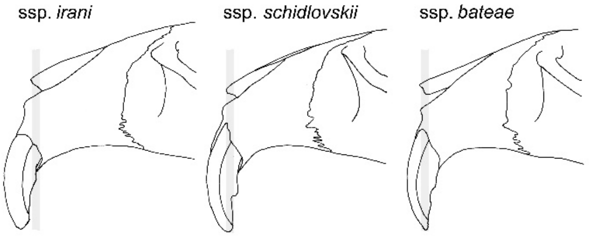


Figure 318: Rostrum (lateral view) in subspecies of *M. irani*: left–ssp. *irani* (Shiraz, Iran), middle–ssp. *schidlovskii* (Gori, Georgia), and right–ssp. *bateae* (Hors Eden Nature Reserve, Tripoli, Lebanon). Grey line is set at the nasal tip to help visualise the degree of proodonty of the incisor. Not to scale.

Microtus irani schidlovskii Argyropulo, 1933

Microtus (Sumeriomys) colchicus schidlovskii Argyropulo, 1933:182. Type locality: "Near the Station Nalband (Transcaucasian Railway), north-east [correctly north-west] Armenia, 1,200 m a. s. l."

Taxonomy. The opinion that *schidlovskii* is part of *irani* is novel (Zorenko et al. 2014). Earlier on, *schidlovskii* was kept within the scope of *socialis* or as a species in its own right. Musser & Carleton (2005) retained *colchicus* Argyropulo and *goriensis* in the synonymy of *schidlovskii* (we tentatively list these names under *socialis*). Cross-breeding trials between *irani schidlovskii* and *socialis satunini* (reported as *binominatus*) yielded fertile females and sterile males (summarised in Zorenko 2013).

Distribution. South-eastern Georgia, Armenia, eastern Turkey and likely extreme north-western Iran.

Characteristics. A larger subspecies with a proportionally short tail (TL/H&B≈0.25). Dimensions: H&B=100–112 g, TL=25–34 mm, HF=14–16.4 mm, EL=8–9 mm, CbL=23.3–26.1 mm, ZgW=14.3–15.2 mm, MxT=5.2–5.7 mm (Argyropulo 1933). Hair is silky, dorsal pelage is brown and grizzled with black; flanks are shaded buff and the demarcation towards a whitish-silver belly is frequently distinct. Skull proportions the same as in nominal subspecies (ZgW/CbL≈0.60); nasals are longer and the upper incisors are orthodont (Figure 318).

Microtus irani bateae Kretzoi, 1962

Microtus socialis bateae Kretzoi, 1962:14. Type locality: "Jebel Kammoucha" [Kammouha Jebel], Liban-Nord, Lebanon.

Taxonomy. Krezoi's name was either overlooked (Lewis et al. 1967, Corbet 1978, Musser & Carleton 2005) or retained in the synonymy of *socialis* (Gromov & Polyakov 1977). We synonymise *bateae* with *irani* following Kryštufek et al. (2013).

Distribution. Known from the mountains of Lebanon but the range is likely more extensive.

Characteristics. A moderately large subspecies with a short tail (TL/H&B=0.21–0.24). Dimensions: BWt=27.5–34 g, H&B=107–115 mm, TL=24–25 mm, HF=16.5–17.7 mm, EL=11–11.6 mm, CbL=24.5–26.3 mm, ZgW=14.8–15.2 mm, MxT=6.1–6.3 mm. In comparison with *karamani*, the back is duller, belly is more slate, tail is darker, more bi-chromatic and with a dark terminal brush; the paws are grey-brown. Skull is narrower (ZgW/CbL=0.58–0.61); nasals are longer and the upper incisors are orthodont (Figure 318).

Microtus irani karamani Kryštufek, Vohralík, Zima, Koubínová & Bužan, 2010

Microtus irani karamani Kryštufek, Vohralík, Zima, Koubínová & Bužan, 2010:13. Type locality: "Turkey, Konya Province, 2 km south of Balkusan, 36°44'N, 32°54'E, altitude ca. 1550 m a.s.l."

Distribution. Taurus (Toros) Mts. in southern Turkey.

Characteristics. A large subspecies with a short tail (TL/H&B=0.22–0.28). Dimensions: BWt=34–41 g, H&B=107–123 mm, TL=26–32 mm, HF=16.5–17.8 mm, EL=9.6–11 mm, CbL=27.0–27.6 mm, ZgW=14.6–16.3 mm, MxT=5.7–6.8 mm (Kryštufek et al. 2010). Fur is soft, pinkish-buff to brownish-buff with fawn tints on the dorsal side, grizzled by blackish tips of long hair; belly is whitish to greyish white; demarcation line on flanks is fairly distinct. Feet pale fawn to nearly white. Tail is indistinctly bi-coloured, fawn, white, buff-white, or brownish above (Kryštufek et al. 2010); terminal brush is light cream. Skull is narrower (ZgW/CbL=0.57–0.60); nasals are longer and the upper incisors are orthodont. M^2 with the postero-lingual salient angle LS4 present in ~½ of individuals.

Microtus paradoxus (Ogneff & Heptner, 1928) – Khorasan (Kopetdag) Social Vole

Chilotus paradoxus Ogneff & Heptner, 1928:263. Type locality: "The area of Tschui [Chuli], next to Askhabad [Ashgabat], Kopet-Dag [Mts.], Transcaspian [region]", Turkmenistan.

Taxonomy. The Khorasan social vole was described as a species in its own right, synonymised with *socialis* afterwards, reinstated as a full species in the late 1980s (Zykov & Zagorodnyuk 1988) but synonymised with *irani* over the next 2 decades (Musser & Carleton 1993, Pavlinov 2006). Phylogenetic reconstruction conclusively reinstalled the specific status of *paradoxus* (Kryštufek et al. 2012b) which was not challenged afterwards.

M. paradoxus is a sister species relative to *irani* (Thanou et al. 2020). Despite this, it is osteologically closer to *socialis* and *dogramacii* (Mahmoudi et al. 2017b); *paradoxus* is also close to *socialis* in acoustic communication (Rutovskaya 2019b). Crossbreeding trials between *paradoxus* and 4 subspecies of *socialis* yielded viable offspring but of reduced fertility (Golenishchev et al. 2002); Zykov (1991) reported sterile progeny while hybridising *paradoxus* with *M. socialis nikolajevi* from Crimea.

Distribution (Figure 319). Endemic to the Turkmen-Khorasan Mountain Range (Kopet Dag) marginally occupying the eastern Alborz Mts. and the south-eastern Caspian coast. The entire range covers an estimated 50,190 km² in the provinces of Golestan, Khorassan-e-Rezavi and Khorrasan-e-Shemali in north-eastern Iran, and Ahal and Balkan in Turkmenistan. The Khorasan social vole is a common rodent and is widespread in cereal steppes covered with shrubs and trees at high (>1,000 m) elevations; the elevational range is much wider however, ranging from –10 (Caspian Depression) to 2,250 m. In arid lowlands voles are restricted to river valleys and wet patches on clay or gravelly substrate (Marinina & Babayev 1973, Kucheruk & Khlyap 2005).

Characteristics. A moderately large and short-tailed vole (TL/H&B=0.19–0.27) with 6 (rarely 5) plantar pads. Dimensions: BWt=30–62.5 g, H&B=87–122 mm, TL=21–30 mm, HF=15–20 mm, EL=9–13 mm, CbL=24.2–30.1 mm, ZgW=14.0–17.9 mm, MxT=5.3–6.8 mm. Pelage is soft; hairs are 6–9 mm long and sparse longer hairs measure 8–13.5 mm; pencil at the tip of the tail is short (1–3 mm) and consists of few hairs. Dorsal fur is light-brown, occasionally with rusty or greyish tint and grizzled by yellowish and blackish tips of longer hairs. Flanks are lighter and more clearly buffy-yellow; some voles are distinctly three-coloured; the belly is grey. Ears are grey, paws are light whitish-grey and the tail is indistinctly bi-chromatic greyish-brown. Skull shows no peculiarities in size or proportions (ZgW/CbL=0.57–0.61), except for a wide interorbital

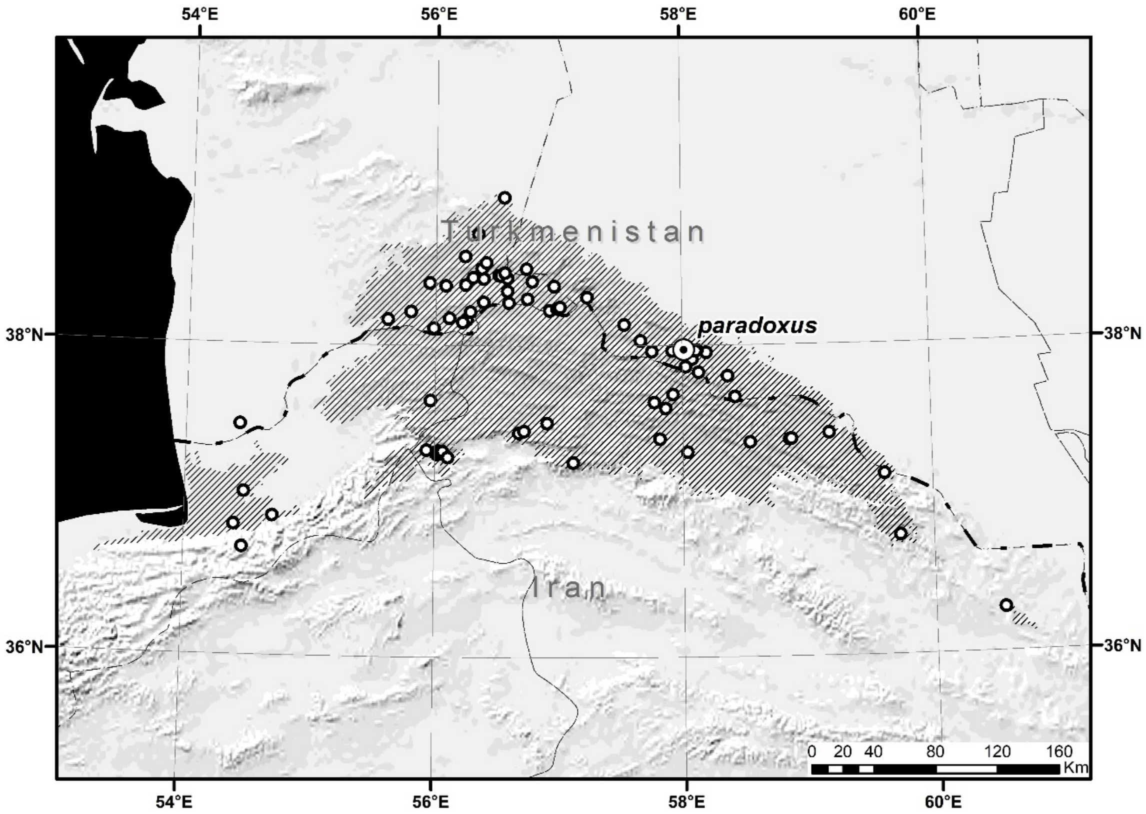


Figure 319: Distributional range of the Khorasan social vole *Microtus paradoxus*.

constriction (width=4.0–4.6 mm) and proportionally long bullae (bullae length/CbL=0.32–0.40) with a swollen mastoid chamber (Figure 316). The upper molars are rather complex: M^1 has an ill-defined postero-lingual salient angle LS4 present in ~40% of voles; the LS4, however, is well-developed in ~90% of M^2 specimens and its dental field is closed in >50% of them. The 3rd upper molar has 3 re-entrant angles on the lingual side and 2 deep re-entrant angles on the buccal side; additional buccal re-entrant angles (BR3 and rarely BR4) are shallow; triangle T4 is confluent with the heel. M_1 has 4 outer and 5 inner re-entrant angles; the antero-labial salient angle BS3 on M_3 is usually present but is rudimentary (Figure 317c). Glans penis is on average 4.2 mm long and 2.2 mm wide (Zorenko 2013). The proximal baculum is 2.70–3.65 mm long and 1.55–1.95 mm wide across the base. The central and lateral distal digits are of approximately the same length (0.95–1.10 mm; Aksenova 1983, Golenishchev et al. 2002). The sperm head is 6.0–7.9 µm long and 4.6–5.8 µm wide (Zorenko 2013).

Karyotype: 2n=62, NF_a=60; all chromosomes are acrocentric (Zykov & Zagorodnyuk 1988, Mahmoudi et al. 2014b).

Variation and subspecies. Monotypic.

Subgroup *guentheri*

Medial metatarsal pad is large, comparable in size to interdigital tubercles; 2n≤54 (karyotype not known in *mustersi*). The subgroup occupies the western portion of the range from south-eastern Europe and Cyrenaica (Libya) to north-western Iran. Basal dichotomy (*guentheri*+*mustersi* vs. *hartingi*+*dogramacii*) dates to 0.6 Mya and the recent species diverged 0.4–0.5 Mya (Thanou et al. 2020).

Microtus guentheri (Danford & Alston, 1880) – Levant (Guenther's) Social Vole

Arvicola guentheri Danford & Alston, 1880:62. Type locality: "marshes below Marash [Kahramanmaraş]", Asia Minor , Turkey.

Synonyms. *Microtus philistinus* Thomas, 1917.

Taxonomy. Taxonomic scope of *guentheri* varied over time. When not synonymised with *socialis*, *guentheri* was understood to include large, short-tailed social voles with 54 chromosomes. Reliance on the karyotype blurred the distinction between *guentheri, hartingi* and *dogramacii* which share the same diploid number. Taxonomic complexity of the entire *guentheri* group became fully understood only with the application of molecular markers (Kryštufek et al. 2009, Thanou et al. 2020).

Distribution (Figure 320). Known with certainty from the eastern Mediterranean region (Levant coast) in Turkey (provinces of Kahramanmaraş, Hatay, Diyarbakır, Gaziantep, Kilis, Mardin, and Şanlıurfa), Lebanon (El Béqaa, Liban-Nord, Mont Liban and Nabatîyé), western Syria (As Suwayda', Al Qunaytirah, Dar'a. Halab, Hamah, Hims, Idlib, Tartus), Jordan (Ajlun, Al Balqa', Al Mafraq, Amman, Irbid, Jarash, Mardaba), Israel (Hadarom, Hamerkaz, Hazafron, Hefa, Tel-Aviv) and West Bank. The range is estimated to cover 108,060 km^2 and the elevational range is from below sea level (–27 m) up to 1,850 m a.s.l. Levant social voles occupy open habitats such as fallow and grain fields, pastures, and high mountain meadows. Preferred are shaded sites with high and dense vegetation, including marshes.

Description (Figure 309d). A large social vole with a short tail (TL/H&B=0.18–0.29). Dimensions: BWt=30–80 g, H&B=103–145 mm, TL=20–35 mm, HF=16–22 mm, EL=10.5–14 mm, CbL=26.9–31.0 mm, ZgW=14.9–19.3 mm, MxT=6.2–7.7 mm. There are 6 palmar pads; the medial metatarsal pad is larger than the interdigital pads and the lateral metatarsal pad is decidedly smaller or occasionally missing (Figure 310d). Fur is moderately soft and rather short, measuring 8.5–10 mm in length with sparse longer hairs measuring 9.5–12 mm. Tail is hairy with a short pencil (length=1.2–1.8 mm). Dorsal pelage varies from fawn to brown and is on average duller than in *hartingi* (see below). Flanks are clear buff, belly is grey and washed buffy in some individuals; the demarcation on flanks is blurry. Tail is sharply bi-

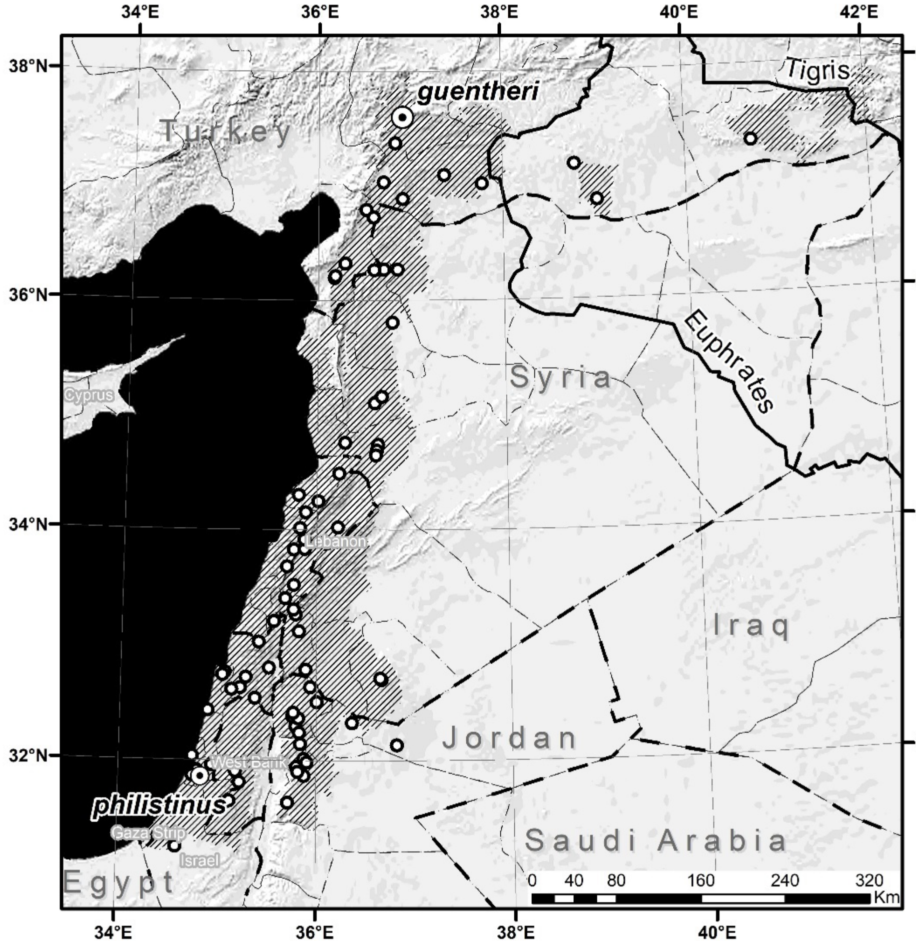


Figure 320: Distributional range of the Levant social vole *Microtus guentheri*.

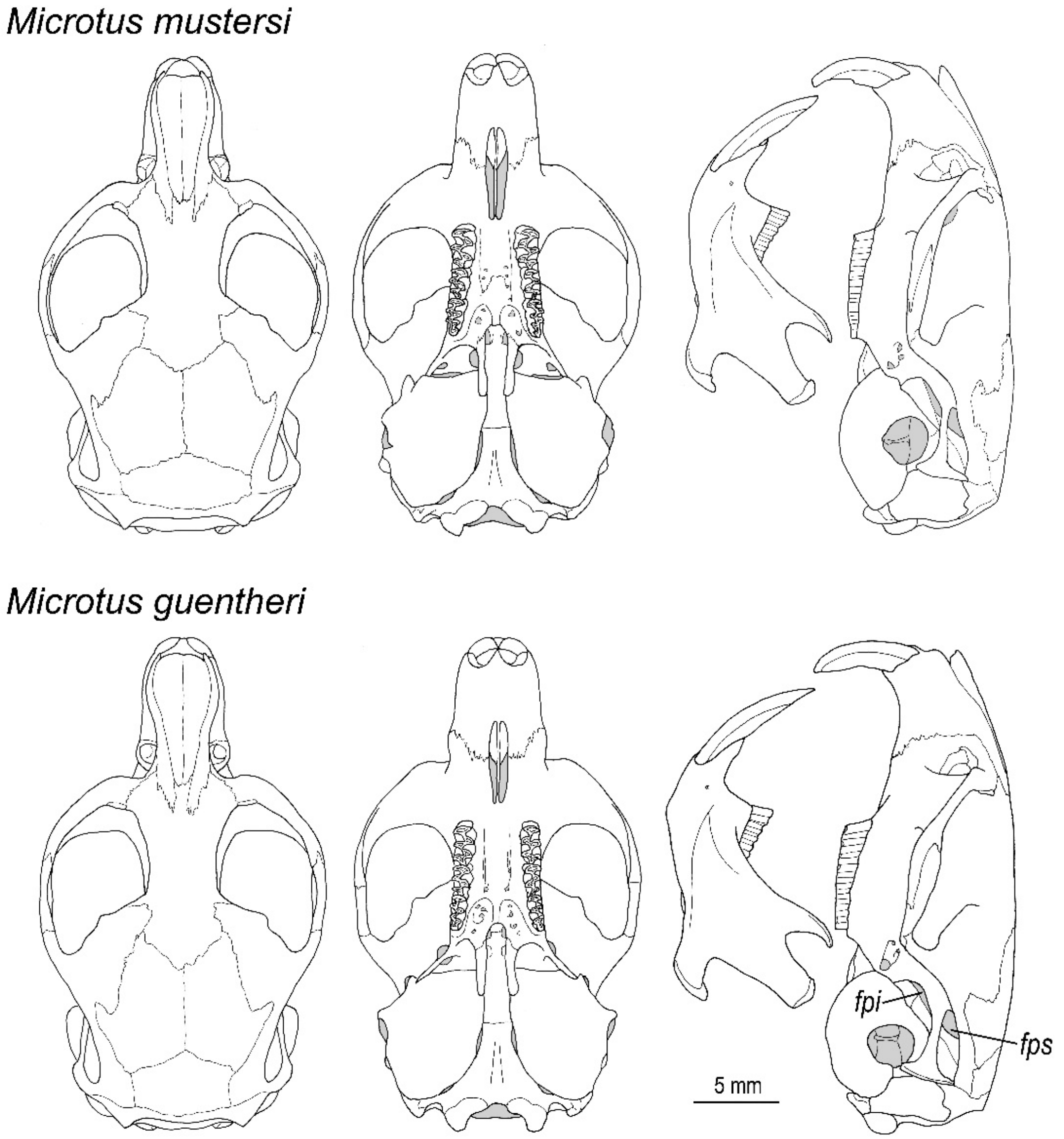


Figure 321: Skull in social voles: top–*Microtus mustersi* (Merg, Cyrenaica. Libya); bottom–*M. guentheri* (Chouf Cedar Reserve, Lebanon). Praelambdoid fenestrae: *fpi–fenestra praelambdoidea inferior*; *fps–fenestra praelambdoidea superior*.

chromatic, blackish-brown above and grey below; ears are grey to blackish-brown and feet are cream. The proximal baculum is 2.48–3.18 mm long and 1.19–1.57 mm wide (Kıvanç 1978); length of distal baculum is 1.19 mm (central digit) and 1.00 mm (lateral digit; Golenishchev et al. 2002). The bacular base is triangular with a prominent medial protuberance directed posteriorly (Yiğit & Colak 2002, Gözütok & Albayrak 2020). Dimensions (length×width) of the sperm head are 7.0–9.0 µm×4.9–5.6µm (Zorenko 2013). The skull is large and deep with well-bent zygomatic arches (ZgW/CbL=0.55–0.62). Temporal ridges are weak and remain apart. The auditory bullae are small (Figure 321), their length accounting for 28.5–33.5% CbL ($\bar{x}$=30.2%). The medial spine of the posterior palate is narrow and well-defined; the lateral pits are deep. Molars: M^2 usually lacks the postero-lingual salient loop LS4. M^3 has 3–4 salient angles on either side; the most common condition is 4 lingual and 3 labial salient angles; the 4th lingual salient angle LS5 is present in 15% of voles; the postero-buccal BS4 is weak. M$_1$ is remarkably invariant showing 5 alternating triangles. The anterior salient angles LS5 and BS4 open into AC (Figure 322a,b). The antero-buccal salient angle BS3 on M$_3$ is well-developed. Karyotype: 2n=54, NF$_a$=52; the X chromosome is acrocentric (Kefelioğlu 1995, Zima et al. 2013).

Variation and subspecies. Possibly monotypic. A report by Lewis et al. (1967) of 3 morphological types in Lebanon, each occupying its own elevational belt, possibly reflects taxonomically mixed material containing *irani* and *guentheri*.

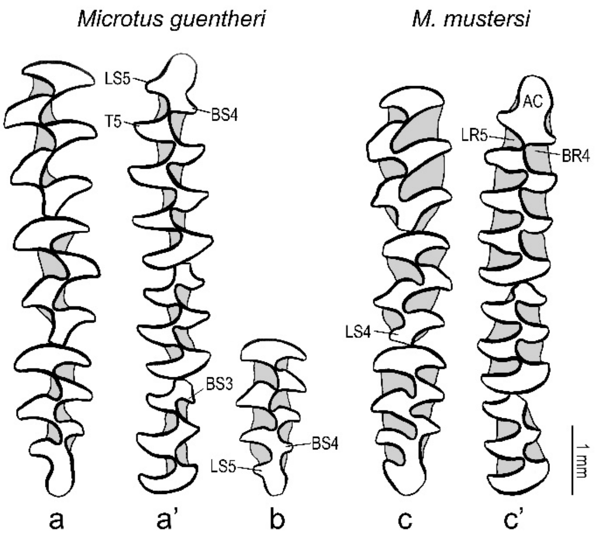


Figure 322: Molar pattern in social voles. *Microtus guentheri* from Chouf Cedar Reserve, Lebanon: upper (a) and lower row (a'); isolated M^3 (b). *M. mustersi* from Merg, Cyrenaica. Libya: upper (c) and lower row (c').

Microtus mustersi Hinton, 1926 – Muster's Social Vole

Microtus mustersi Hinton, 1926b:305. Type locality: "Merg, Cyrenaica. Altitude 300 m", Libya.

Taxonomy. Described as a species in its own right but since the late 1940s synonymised with *guentehri* or *irani*. *M. mustersi* is a sister species to *guentheri* (Thanou et al. 2020).

Distribution (Figure 323). Range (area=11,560 km^2) is restricted to the Cyrenaican Plateau in north-eastern coastal Libya, i.e. to the districts of Al Hizam al Akdar, Al Jabal al Akhdar, and Al Marj. Lives in flat and hilly landscape at low elevations (<825 m), on hard and frequently rocky ground; preferred are moist sites and dense grassy and shrubby cover; also present on cultivated soil. Habitat is sporadic and local and the abundance is low (Ranck 1968).

Muster's social vole is the only recent arvicoline in Africa where its presence dates back to the Pleistocene (Ranck 1968, Pardiñas et al. 2017). Cyrenaica social voles from the Earlier Palaeolithic were described as a distinct species *M. cyrenae* Bate, 1955. Taxonomic

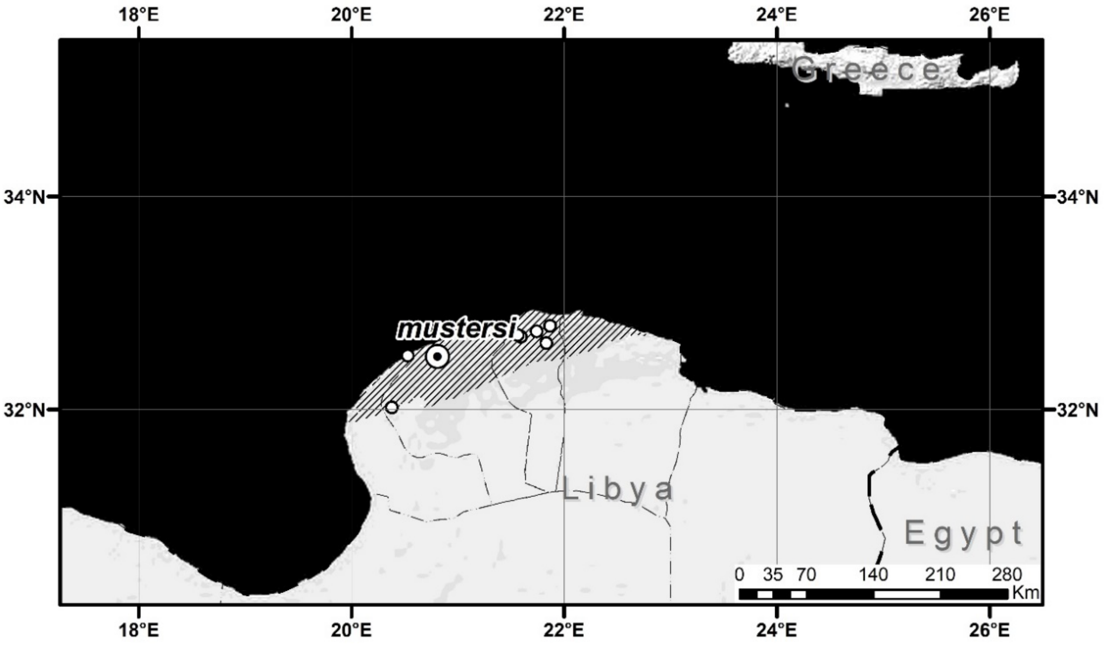


Figure 323: Distributional range of Muster's social vole *Microtus musteri*.

recognition was justified by their smaller size and minor dental differences.

Characteristics. Dimensions: BWt=27–46 g, H&B=102–117 mm, TL=20–33 mm, HF=15.5–22 mm, EL=9.5–13 mm, CbL=26.5–28.7 mm, ZgW=15.6–17.2 mm, MxT=6.4–7.0 mm. Similar to *guentheri* but smaller; tail of approximately the same relative length (TL/H&B=0.19–0.30). There are 5 plantar pads and the medial metatarsal pad is large; plantae are naked. Fur is soft, dense and moderately long (6.5–7.0 mm; longer dark-tipped hairs measure 8.4–9.7 mm); tail is hairy with a short pencil (length=1.7–2.4 mm). Ears are inconspicuous and sparsely hairy. Dorsal pelage is uniformly rich yellowish-brown to cinnamon-red and finely speckled by dark hair tips. Flanks are lighter, usually clear ochraceous-buff and the demarcation towards the belly is rather distinct. Ventral hairs are white-tipped but their bases are slate. The tail is bi-chromatic, brownish above and cream or buffy below; the ears are dull brownish and the paws are yellowish-white. The skull is on average smaller than in *guentheri* but of similar proportions (ZgW/CbL=0.59–0.61); bullae are slightly longer and the incisive foramina are longer (Figure 321). Molars: approximately half of voles (=47%) bear the postero-lingual salient loop LS4 on M^2; M^3 has 3–4 labial salient angles (Figure 322c). The remaining molars are essentially as in *guentheri*. Karyotype is not known.

Variation and subspecies. Monotypic.

Microtus hartingi Barrett-Hamilton, 1903 – Harting's Social Vole

Microtus (Microtus) hartingi Barrett-Hamilton, 1903b:307. Type locality: "Larissa, Thessaly" (p. 308), Greece.

Synonyms. *Microtus lydius* Blackler, 1916; *Microtus (Sumeriomys) güntheri shevketi* Neuhäuser, 1936; *Sumeriomys guentheri martinoi* Petrov, 1939 [preoccupied by *Pitymys nyirensis martinoi* Éhik, 1935 (=*Microtus subterraneus*)]; *Microtus guentheri strandzensis* Markov, 1960; *Microtus guentheri macedonicus* Kretzoi, 1964 [new name for *martinoi* Petrov (the author's name and the year are incorrectly given as Popov 1941)]; *Microtus lydius ankaraensis* Yiğit & Çolak 2002.

Taxonomy. Vouchers of Harting's social voles from Thessaly, Greece, sent to the Natural History Museum in London were at first identified by O. Thomas as (*Arvicola*) *guentheri* (Harting 1899), subsequently recognised as representing a new species (Barrett-Hamilton 1903b) and again synonymised with *guentheri* (Neuhäuser 1936b). The status of a species in its own right was re-established for *hartingi* after 2000, firstly on morphological grounds (Yiğit & Colak 2002) and subsequently confirmed in *Mt*-DNA phylogenetic reconstruction (Kryštufek et al. 2009). European and Anatolian Harting's voles are genetically close (Kryštufek et al. 2009, Thanou et al. 2020) and hybridise in captivity. The hybrids, however, showed lower spermatogenetic activity and males obtained in backcrossing trials were sterile and less viable. On these grounds Zorenko et al. (2016) called for taxonomic separation of the European voles (as *strandzensis*) from the Asiatic ones (*lydius*). The name *lydius* was occasionally used for the Asiatic Harting's social voles (Yiğit & Colak 2002, Grimmberger et al. 2009).

Distribution (Figure 324). Range with an area of 209,650 km² occupies south-eastern Europe (southernmost Serbia, North Macedonia, Greece, south-eastern Bulgaria, and Turkish Thrace) and western, central, and southern Anatolia (Turkey in Asia) as far east as the line Tokat–İçel. In Europe, the Harting's social vole is likely a fairly recent newcomer from Anatolia. The range is highly fragmented with at least 7 major fragments in south-eastern Europe and further smaller isolates in between. The largest fragments are in (i) the Vardar Valley in North Macedonia, (ii) Thessaly (iii), Sterea Ellada (both in Greece), and (iv) the Strandzha Mts. (Burgas) in Bulgaria. Results of habitat modelling for Harting's social vole suggest a collapse of its European range in a matter of decades (Kryštufek et al. 2018). Present on 2 islands: St. Thome (Black Sea offshore Bulgaria) and Lesbos (Aegean archipelagos, ~5.5km off the Anatolia coast). Altitudinal range is 0–1,950 m.

Characteristics (Figure 309f,g). Dimensions: BWt=30–78 g, H&B=103–138 mm, TL=20–35 mm, HF=18–21.6 mm, EL=10–14 mm, CbL=27.2–31.1 mm, ZgW=15.3–18.2 mm, MxT=6.5–8.0 mm. General appearance and proportions as in *M. guentheri*; TL/H&B=0.18–0.27. There are 5 palmar pads and the presence of the tiny lateral metatarsal pad is rare (in ~2% of voles); the sole is furred posterior to pads (310e,f)). Fur is moderately soft and slightly longer (7.5–11.5 mm) than in *guentheri*; sparse longer hairs measure 10.5–13.5 mm. Tail is hairy and the underlying annulation is barely visible; terminal pencil measures 1.5–3.0 mm. Pelage is on average lighter than in *guentheri*. Dorsal fur is yellowish-brown to light buff, shaded grey in some local populations. The overall appearance is grizzled due to black hair tips on the back but becomes clear on the flanks and thighs. Underside is grey with blotches formed by white-tipped hairs; it is irregularly clouded with slate hair bases and some individuals show buffy shade. Young voles are duller. Feet are cream and ears are grey. Tail is bi-chromatic in the majority of individuals though demarcation between the blackish dorsal and the cream ventral sides is rarely sharp. Glans penis (length=4.3±0.19 mm; width= 2.8±0.10 mm; Zorenko 2000, 2013) is like in *guentheri* (Yiğit & Colak 2002). Proximal baculum is 2.75 mm long and 1.43 mm wide across the base; Length of distal baculum is 1.09 mm and 1.04 mm for central and lateral digits, respectively (Zorenko 2013). The proximal baculum is smaller in coastal Anatolia (length×width=2.3×1.0 mm) and larger in Central Anatolia (2.9×1.5 mm; Yiğit & Colak 2002, Gözütok & Albayrak 2020). The base of baculum is rounded, occasionally with a medial notch on the posterior margin. Sperm head is 6.0–8.6 μm long and 4.3–5.3 μm wide (Zorenko 2013).

The skull is essentially as in *guentheri* (ZgW/H&B=0.54–0.62) with a slightly deeper rostrum. Also, the auditory bullae are comparatively larger than in *guentheri* (Figure 325). The medial spine of the posterior palate is broad and the lateral pits are shallow. Molars: M^2 usually lacks the postero-lingual salient loop LS4; its frequency is rarely >10%. M^3 as in *guentheri*: ~85% of voles have 4 inner and 3 outer salient angles but some populations deviate significantly from this figure. M_1 is as in *guentheri*; the

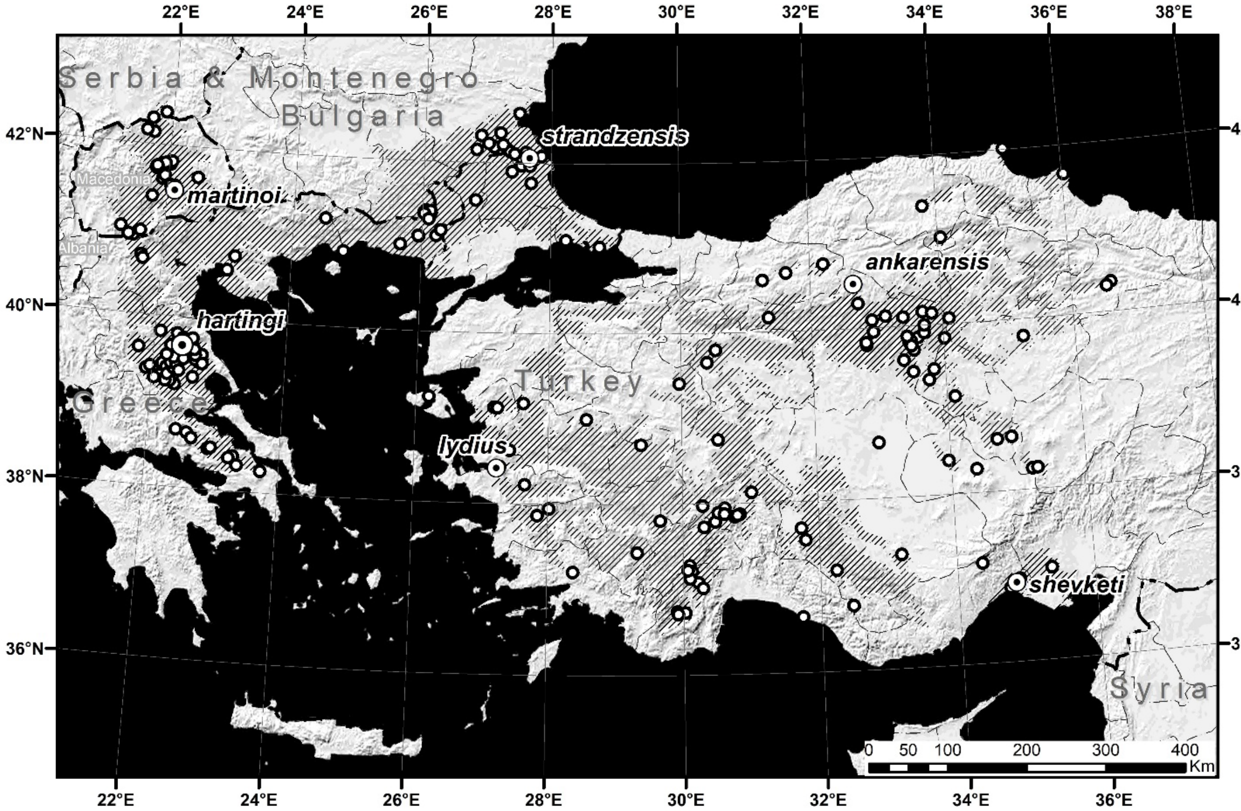
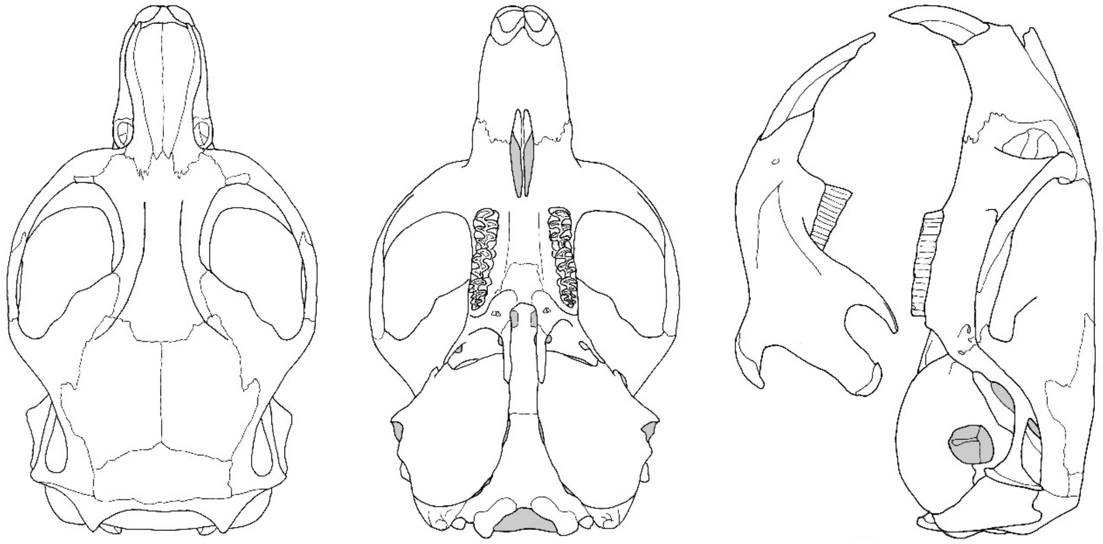


Figure 324: Distributional range of Harting's social vole *Microtus hartingi*.

Microtus dogramacii



Microtus hartingi

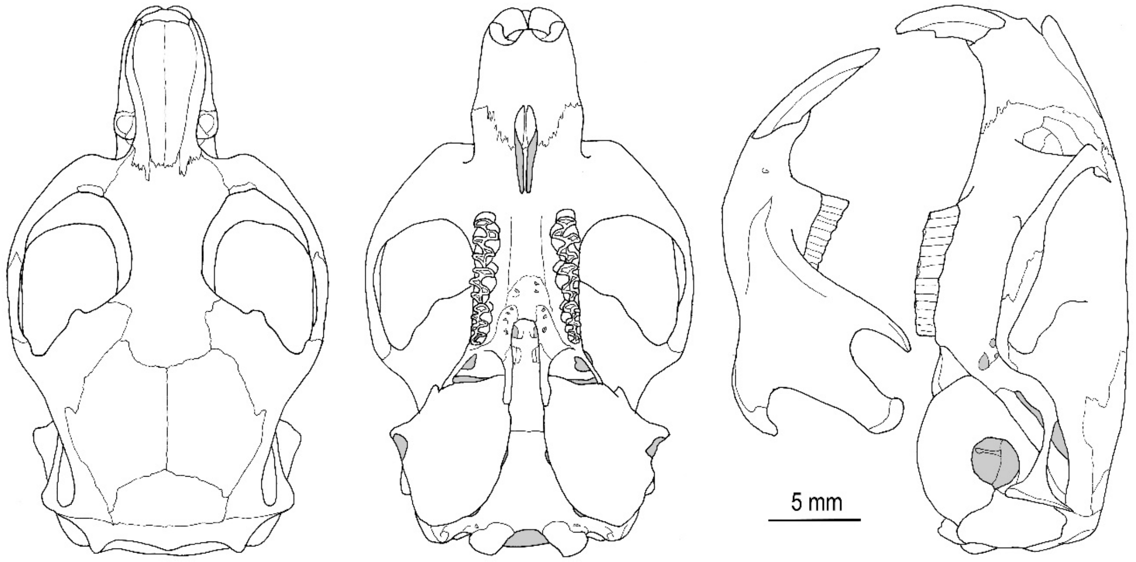


Figure 325: Skull in social voles: top–*Microtus dogramacii* (Qazvin Province, Iran); bottom–*Microtus hartingi* (Gradsko, North Macedonia).

antero-labial salient angle on M_3 (BS3) is rudimentary (Figure 326a-c'). Karyotype: 2n=54, NF_a=52; the X chromosome is acrocentric or bi-armed (Mitsainas et al. 2010, Zima et al. 2013).

Variation and subspecies. Comparisons between voles from the opposite sides of the Bosporos Strait retrieved a number of differences between studied samples. E.g., the sperm head is smaller in voles from Anatolia (length×width=6.98×4.70 µm) and larger in those from the Balkans (7.25×5.06 µm; Zorenko 2013). The former are monogamous with no communal nest building and the latter are both monogamous and polygamous with communal nests (Romanosa 2019). Similar differences were reported for traits used in traditional taxonomy (fur colouration, size, incidence of T5 on M^2) but with little evidence on the generality of observations which would justify the application of trinomial taxonomy. Molecular evidence suggests a fairly recent vicariance at the Bosporus Strait and phylogeographic structuring into 5 lineages: 2 lineages in Europe, 1 lineage in Anatolia, and 2 lineages in the Lesvos where they occupy opposite sides of the island. With all this in mind we are hesitant to propose a formal trinomial taxonomy for *hartingi*.

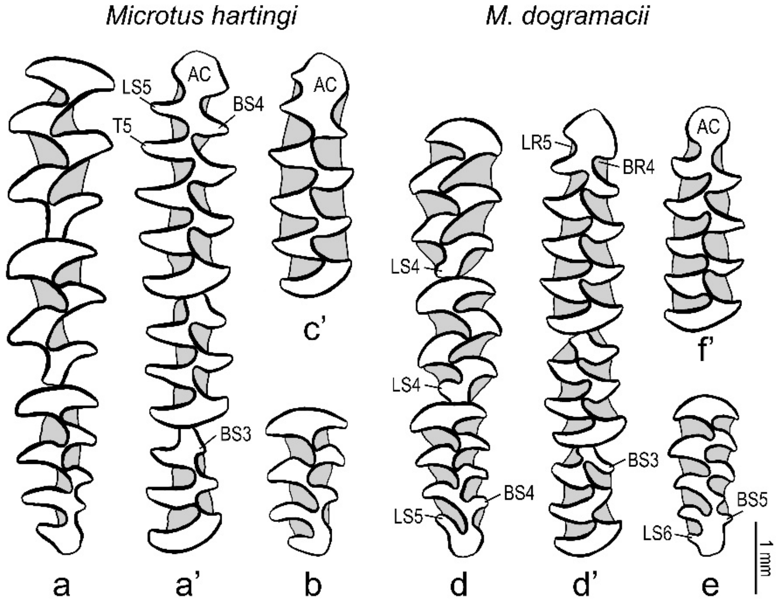


Figure 326: Enamel molar pattern in social voles. *Microtus hartingi*: upper (a) and lower row (a'–Gradsko, North Macedonia) and isolated M^3 (b–Eğirdir, Turkey) and M_1 (c'–Burdur, Turkey). *M. dogramacii*: upper (d) and lower row (d'–Diyarbakır, Turkey) and isolated M^3 (e–Harran, Turkey) and M_1 (f'–Harran, Turkey).

Microtus dogramacii Kefelioğlu & Kryštufek, 1999 – Dogramaci's Social Vole

Microtus dogramacii Kefelioğlu & Kryštufek, 1999:301. Type locality: "Turkey, Amasya, Suluova, Boyali köyü (35°36'E, 41°40'N); altitude 900 m above sea level."

Synonyms. *Microtus (Sumeriomys) qazvinensis* Golenishchev, 2002; *Microtus elbeyli* Yiğit, Çolak & Sözen, 2016.

Taxonomy. Three different names were proposed for Dogramaci's social vole over the last ~2 decades (*dogramacii*, *qazvinensis*, *elbeyli*) and their taxonomic relationships were gradually disentangled via a series of phylogenetic analyses (Jaarola et al. 2004, Kryštufek et al. 2009, Mahmoudi et al. 2014a). Molecular evidence showed that *dogramacii* and *qazvinensis* are conspecific (Pardiñas et al. 2017). Naming *elbeyli* as a species new to science was justified by the peculiarities of the karyotype and cranial and dental morphology (Yiğit et al. 2016). Its molecular makeup is still not known, the exposed traits are nevertheless within the variation range for *dogramacii*. In its current scope, *dogramacii* is a sister species to *hartingi* (Mahmoudi et al. 2014a).

Distribution (Figure 327). The range (area=265,120 km^2) is continuous in north-western Iran (as far east as the line Tehran–Lorestan–northern Ilam) from where it stretches across northern Iraq (where social voles are present but not yet securely identified) into south-eastern Turkey (Şanlıurfa, Çeylanpınar, and Elazığ) as far north as the Murat River. Distributional details are meagre along the Levant coast but the vole indisputably reaches northern Jordan (Thanou et al. 2020). Also present in south-western Iran (Fars) and in Central Anatolia (provinces of Amasya, Aksaray, Çorum, and Samsun). Altitudinal range is 130–2,440 m.

Description (Figure 309c). Dimensions: BWt=20–65 g, H&B=98–126 mm, TL=18–39 mm, HF=14–21 mm, EL=9–15 mm, CbL=24.1–29.9 mm, ZgW=14.1–18.1 mm, MxT=5.4–6.6 mm. Similar to *guentheri-hartingi* except smaller; the tail is similarly short (TL/H&B=0.17–0.34) with 5 palmar pads. Fur is soft, 9.5–10.5 mm long and the exposed black-tipped hairs stretch for another ~1 mm. The tail is hairy with an ill-defined and short (length=1.2–1.8 mm) pencil. Dorsal fur varies between ochraceous-brown to pale reddish-brown; it is grizzled by black hair-tips but the flanks are frequently plain buff; demarcation towards the greyish-white underside is sharp in some individuals;

belly is usually shaded buff. Feet are cream to light grey, ears are grey and the tail is bi-chromatic, yellowish-brown to dark brown above and dirty white below. The baculum is similar as in *guentheri*; the proximal bone measures 2.63 mm and has a broad base (width=1.48 mm) with a triangular posterior profile (Çolak et al. 1997, Gözütok & Albayrak 2020). The skull is similar to *hartingi*; bullae tend to be longer and the skull is slightly shallower (Figure 325). The medial spine of the posterior palate is high and the lateral pits are deep. The alveolar process protrudes on the lingual side of the mandibular ramus. Molars show a complex enamel pattern (Figure 326d-f'): an additional postero-lingual salient angle (LS4) on M^2 is prominent in 75–100% of individuals; a similar although less protuberant salient angle is also occasionally present on M^1. M^3 is complex and in >50% of voles with 4 salient angles on each side; ~10% of animals have 5 lingual salient angles. M_1 as in *hartingi*; the antero-labial salient angle BS3 on M_3 is noticeable.

Dogramaci's social vole is the only social vole with a polymorphic karyotype: 2n=46, 48, 54. Voles from north-western Iran show a standard karyotype identical to *guentheri-hartingi*: 2n=54, NF_a=52; all autosomes are acrocentric (Mahmoudi et al. 2014a,b). Populations from Central Anatolia have 2n=48, NF_a=46, 48, 50, and 1 pair (NF_a=48) or 2 pairs (NF_a=46) of bi-armed chromosomes (Kefelioğlu & Kryštufek 1999, Albayrak et al. 2012, Atlı Şekeroğlu et al. 2011). Polymorphism has been ascribed to pericentric inversions and no hybrid voles have been recovered (Atlı Şekeroğlu et al. 2011). Voles from Kilis (southern Anatolia) have 2n=NF_a=46 and a submetacentric X chromosome (Yiğit et al 2016); a similar karyotype but with an acrocentric X was reported from Fars Province (NW Iran; Mahmoudi et al. 2014b). In eastern Anatolia (Harput), 2 males from a 2n=54 population were heterozygous for the centric fusion between two nonhomologous autosomes of different sizes and had 2n=53 (Zima et al. 2013). Dogramaci's social vole differs from *hartingi* in having

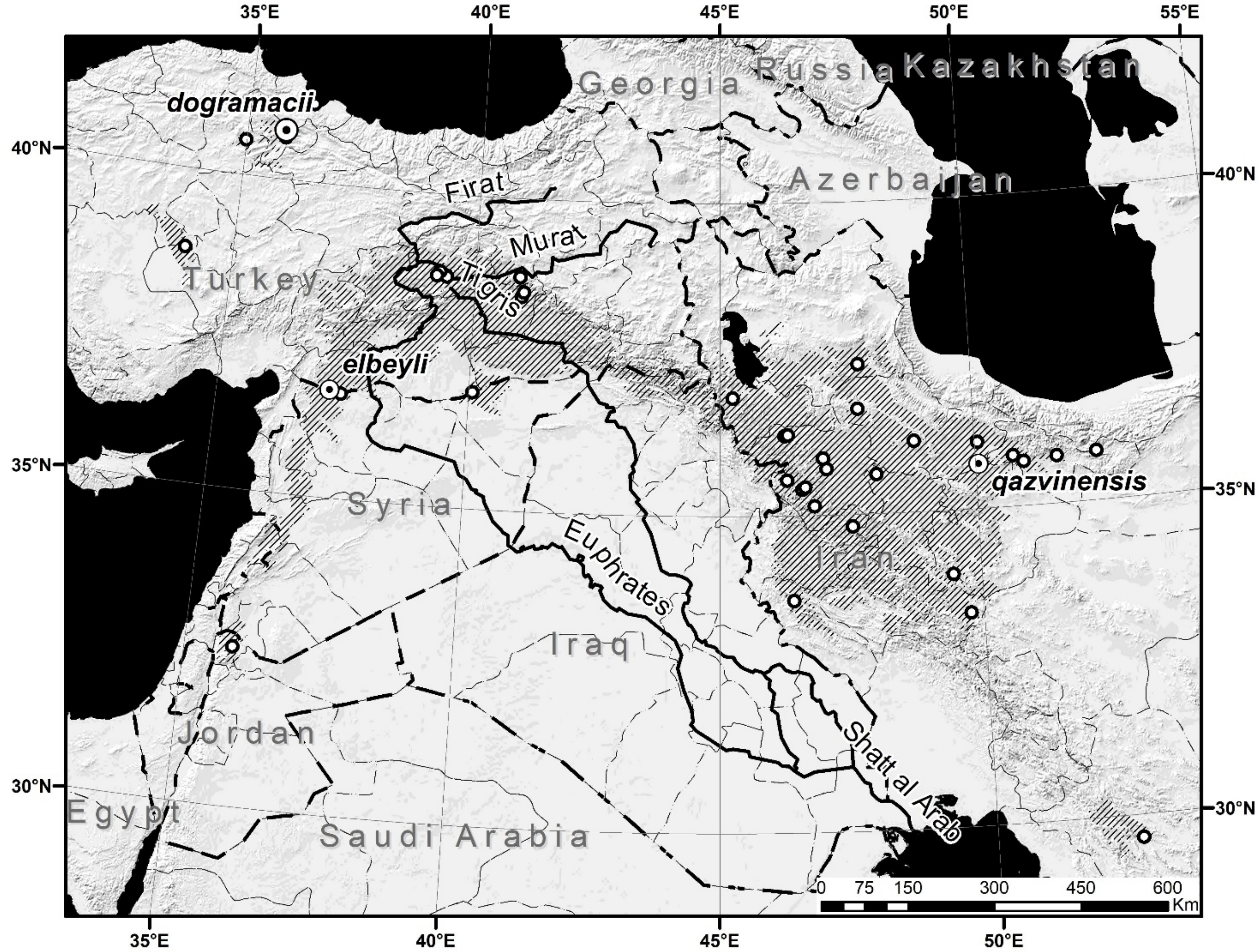


Figure 327: Distributional range of Dogramaci's social vole *Microtus dogramacii*.

a distinct heterochromatic block on the second largest autosome and the C-banding pattern of the X chromosome (Zima et al. 2013, Arslan & Zima 2014).

Variation and subspecies. Phylogenetic analysis assigned Anatolian and Iranian samples into distinct monophyletic sister lineages separated by a pairwise genetic divergence of 2.80 (Mahmoudi et al. 2014a). Morphologically, the eastern populations are more similar to *guentheri-hartingi* than the western samples. Only the western populations show Robertsonian rearrangements while populations from Iran and adjacent parts of Turkey have 2n=54; an exception is the 2n=46 cytotype from Fars, Iran (reported as *irani*; Mahmoudi et al. 2014b). Dogramaci's social vole is obviously polytypic but the pattern of geographic variation is complex and still poorly understood. Aberrant colour morphs were reported from Iran (Mahmoudi et al. 2014a).

Species group *schelkovnikovi*

Contains a single species which in the past was classified as a member of *Pitymys* (Shidlovskiy 1962, Pavlinov & Roosolimo 1987), *Terricola* (Zagorodnyuk 1990, Musser & Carleton 1993, 2005), or *Hyrcanicola* (Nadachowski 2007). Molecular phylogenetic reconstructions (Martínková & Moravec 2012, Steppan & Schenk 2017) retrieved a sister position of *schelkovnikovi* with respect to the *socialis* species group; TMRCA was estimated at 1.24 Mya (Thanou et al. 2020). Because of categorical morphological differences between the two groups, we classify *schelkovnikovi* as the sole member of its species group.

Microtus schelkovnikovi Satunin, 1907 – Schelkovnikov's Vole

Microtus schelkovnikovi Satunin 1907:242. Type locality: "in a forest, on the way to the village Dzhi", Lankoran District, Azerbaijan.

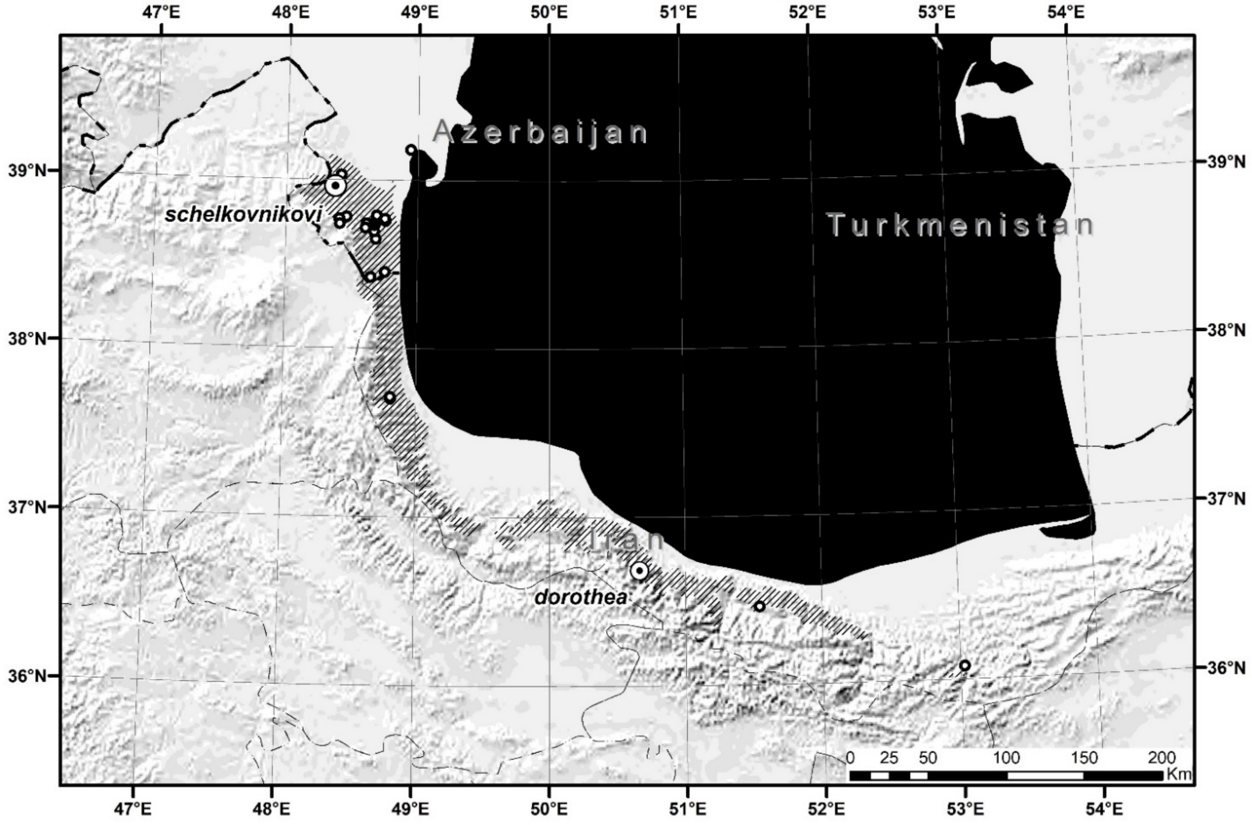


Figure 328: Distributional range of Schelkovnikov's vole *Microtus schelkovnikovi*.

Synonyms. *Pitymys subterraneus dorothea* Ellerman 1948.

Taxonomy. Satunin based *schelkovnikovi* on a single specimen; the skull was heavily damaged and subsequently lost (Ognev 1950). The species therefore remained virtually unknown until the late 1940s (see Shidlovskiy 1938). At first, *schelkovnikovi* was thought to represent *Microtus majori kaznakovi* (Vinogradov 1933, Kuznetzov 1944, Kuznetsov 1965; now a synonym of *Alticola stoliczkanus*); subsequent authors synonymised *schelkovnikovi* with *M. majori* (Vinogradov & Argyropulo 1941, Vereshchagin 1959) or ignored it entirely (Ognev 1950, Vinogradov & Gromov 1952), while Ellerman (1948) named it de novo as a subspecies of *M. subterraneus*. Schelnikov's vole was re-established as a species in its own right by Alekperov (1959).

Distribution (Figure 328). Humid Hyrcanian forests in south-eastern Azerbaijan and north-western Iran (Gilan, Mazandaran), specifically in the Lenkoran lowlands south of the Kura River, and the Talysch Mts. and Alborz Mts. (cf. Nadachowski 2007). Range measures 9,360 km^2 and the elevational range is at -27–1,970 m.

Characteristics. A small and short-tailed common vole; TL/H&B=0.21–0.29. The ears are hidden in the fur, the eyes are minute (palpebral fissure is 1.2–1.7 mm long; Tembotova 2015). Fur is soft, dense and short (length=6–8.5 mm); scattered black-tipped hairs are only slightly (~1 mm) longer. Tail is moderately hairy and terminal brush is sparse (length=2.5–3.5 mm). There are 5 palmar and plantar pads, respectively (Figure 329). Fur is dull rusty brown to dark brown, duller on the head; flanks are lighter and gradually transgress to brown-slate underside; tail is bi-chromatic (dark brown above, grey below), ears are grey and paws are light grey. Females have 8 nipples. Glans penis is ~3 mm long; the baculum was not studied. The skull is short, wide (ZgW/CbL=0.60–0.63) and deep; dorsal profile is evenly convex (Figure 330). Nasals are comparatively short and the interorbital region is wide (4.3–4.7 mm). The mandible shows a heavy coronoid process and a short angular process; the bulge of the alveolar process on the outer

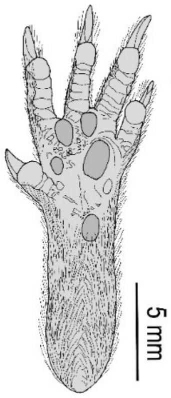


Figure 329: Left sole in *Microtus schelkovnikovi* (Mazandaran, Iran).

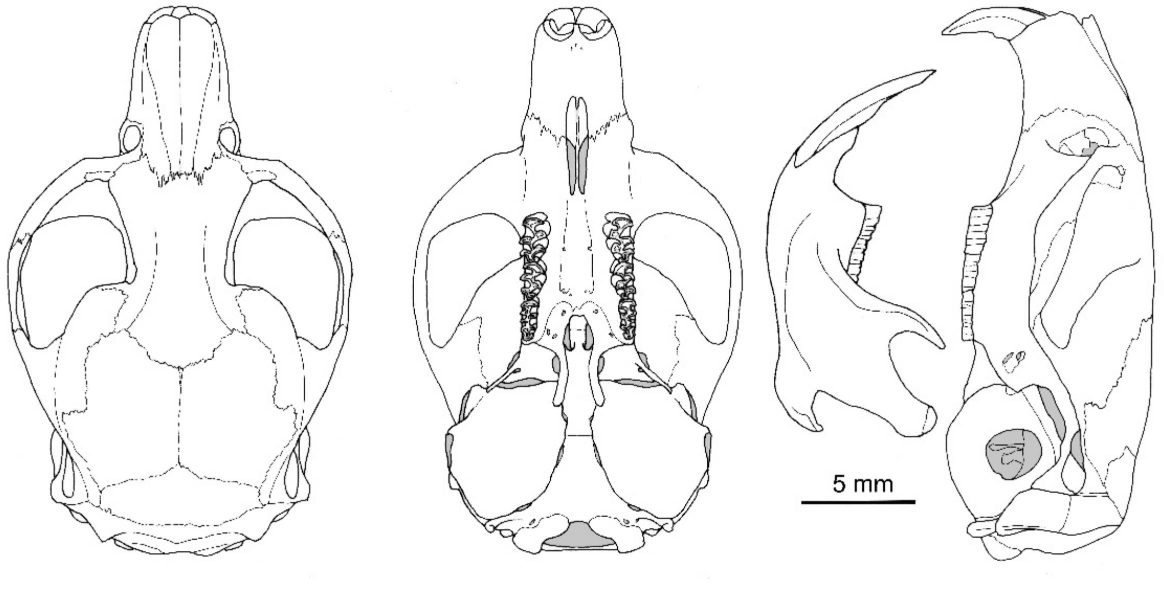


Figure 330: Skull in *Microtus schelkovnikovi* from Lerikskiy Rayon, Azerbaijan.

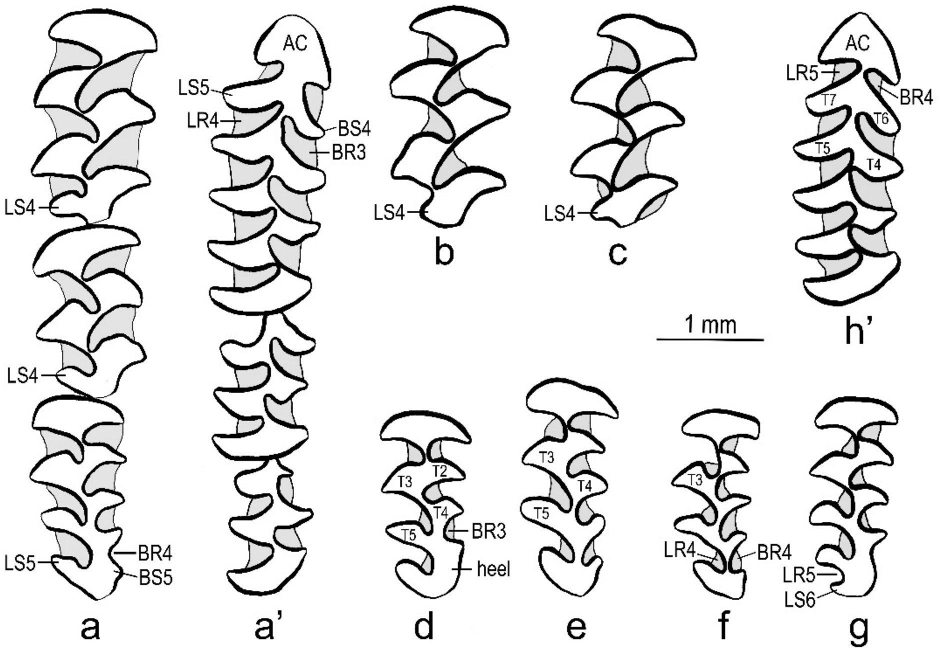


Figure 331: Enamel molar pattern in *Microtus schelkovnikovi*: upper (a) and lower row (a'); isolated M^1 (b,c), M^3 (d–g), and M_1 (h'). Based on vouchers from Lerikskiy Rayon, Azerbaijan (a-a',h'), Weyser, Mazandaran, Iram (b), Asalem, Gilan, Iran (c,e –g), and Dash Lateh, Mazandaran (d).

side of the ramus is ill-defined. Incisors are orthodont; molars are comparatively small. M^1–M^2 have additional postero-lingual salient angles LS4 (T5); the angle is of variable size on M^1 and is always prominent on M^2 (Figure 331a-c). M^3 is highly variable with 3–5 inner and 4–5 outer salient angles; frequently the T2–T5 dental fields are confluent and occasionally merge with the heel. The posterior cap is frequently isolated by deep re-entrant angles LR4 and BR4. M_1: the opposite dental fields T4–T5 and T6–T7 are widely confluent and form transverse prisms. The anterior cap is either confluent with dental fields T6–T7, or isolated by deep re-entrant angles BR4 and LR5 (Figure 331h'). Karyotype: 2n=54, NF_a=60, NF=62; both sex chromosomes are acrocentric (Achverdjan et al. 1992, Kuliev & Bickham 2010).

Variability and subspecies. Rarely, *dorothea* is treated as a distinct subspecies on grounds of its putative smaller size (Gromov & Polyakov 1977, Pardinas et al. 2017). When described, *dorothea* was diagnosed against *M. subterreanes* and *majori* and was not compared with *schelkovnikovi* from Azerbaijan.

Bibliographic list

Transliteration

The papers quoted below have been published in various languages and scripts found across the Palaearctic Region. Many important works are in Slavic languages (in particular Russian), Chinese, Korean, and Japanese, to mention just the main linguistic groups. Whenever these papers have a title written in English or another language widely used in the past by the zoological community (Latin, German, French and so on), we quoted it. The remaining titles were translated and are in square brackets.

The names of the authors were not always consistently transliterated into the Latin script. We have retained transliterations as they were originally used in the quoted papers. For this reason, the spelling of the same name may vary (e.g. Kozlovsky or Kozlovskij; Meier or Meyer; Ognev or Ogneff, etc.).

Abbreviations

AN USSR – Academy of Sciences, Union of the Soviet Socialist Republics (in use before 1991); national academies used the name of a Republic followed by the SSR (the Soviet Socialist Republic; e.g. Belorussian SSR or BSSR) or ASSR (Autonomous Soviet Socialist Republic)
ICZN – International Commission on Zoological Nomenclature
RAS – Russian Academy of Sciences (in use after 1991)

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Appendix

Chionomys stekolnikovi Golenishchev, Malikov, Bannikova, Zykov, Yiğit & Çolak, 2022:8. Type locality: "Turkey, Central Taurus Mts., Aladaglar Range, 3.5 km west from Karanfil Mt. (37.6084°N, 35.0044°E), 1709 m a.s.l., from the edge of a slope in a meadow with stony soil and bushes".

The new species is based on cyt*b* sequences of two vouchers collected 3.5 km apart in the Central Taurus Mts., Turkey. The highly divergent cyt*b* haplotype of the type specimen was in the past erroneously aligned with *C. n. spitzenbergerae* (Bannikova et al. 2013) and is now named as a new species of snow voles; the earlier misclassification was corrected by Arslan et al. (2017). While mitochondrial divergence between *stekolnikovi* and published haplotypes of *C. nivalis* is impressive, it does not match the divergence yielded from two nuclear genes (*BRCA1* and *GHR*). This discrepancy is left unexplained in the paper by Golenishchev et al. (l. c.). Craniometric analysis was based on minuscule hypodigmas (only six skulls were available from Turkey) and did not retrieve a noteworthy difference between *stekolnikovi* and *C. nivalis*. Molar pattern was not addressed. Having in mind conflicting phylogenetic scenario resulting from different molecular markers one would wish first to assess phylogeographic pattern before basing a new species entirely on genetic evidence. Quite surprisingly, Golenishchev et al. (l. c.) paid no attention on the lack of molecular data on *C. nivalis* from Central Anatolia. Kryštufek & Vohralik (2005) showed that snow voles from the vicinity of Kaiseri (Ercyes Dağı and Talas) and Elazığ differ morphologically from other subspecies of *C. nivalis* in Turkey though they did not use a formal trinomen for them. Snow voles from the vicinity of Kaiseri would be an obvious necessity for any taxonomic or phylogenetic study because of their immediate proximity to the type locality of *stekolnikovi*. Disentangling the molecular puzzle of snow voles in the Taurus Mts. and building a robust taxonomy of the subgenus *Chionomys* is therefore a task left for the future.

Reference: Golenishchev F.N., Malikov V.G., Bannikova A.A., Zykov A.E., Yiğit N. & Çolak E. (2022). Diversity of snow voles of the "*nivalis*" group (*Chionomys*, Arvicolinae, Rodentia) in the eastern part of the range with a description of a new species. Russian J. Theriol. 21(1): 1–12.

M[icrotus] irani darvishi Mahmoudi, Golenishchev, Malikov, Arslan, Pavlova, Petrova & Kryštufek, 2022 (pagination still not final). Type locality is "near Chellegah village (31°25'N/51°00'E), Lordegan county, Chahar-Mahal & Bakhtiari Province, Iran".

Microtus irani darvishi, with its range in the Province of Chahar Mahall va Bakhtiari, holds a sister position against *M. i. irani* from the Fars Province. The new subspecies differs from *irani* s. str. by its shallower, shorter, and wider rostrum, a shorter mandibular tooth row, a smaller mandible, a shorter and wider frontal incisive foramen, and a smaller tympanic bulla. M^2 lacks postero-lingual salient angle LS4 (T5) which is reported for c. 30% of *M. i. irani*. Karyotype of *darvishi* (2n = NF = 60) is identical to the one reported for irani (see p. 375 above).

Reference: Mahmoudi A., Golenishchev F.N., Malikov V.G., Arslan A., Pavlova S.V., Petrova T.V. & Kryštufek B. (2022). Taxonomic evaluation of the "*irani–schidlovskii*" species complex (Rodentia: Cricetidae) in the Middle East: A morphological and genetic combination. Zool. Anz. 300 (early online), doi.org/10.1016/j.jcz.2022.07.001

Zoobank registrations

ZooBank registration of the present Book: urn:lsid:zoobank.org:pub:5C327A0B-65B7-4BF2-99F0-735357B43B2E

Registrations of nomenclatural acts:

Lemmus lemmus kamchaticus, new subspecies (p. 47)
ZooBank registration: urn:lsid:zoobank.org:act:D8A3B97D-9BEB-4B7B-91AC-311244B7A8C8

Alticola kohistanicus, new species (p. 72)
ZooBank registration: urn:lsid:zoobank.org:act:C9C8C596-E520-4B2D-8E04-924D4959C677

Protochionomys, new subgenus (p. 205)
ZooBank registration: urn:lsid:zoobank.org:act:C693A8E1-E587-4092-8407-49058DBF4D5E

Yushanomys, new subgenus (p. 269)
ZooBank registration: urn:lsid:zoobank.org:act:56D626CF-89FC-4118-B5DF-80B254CBB723

Mictomicrotus, new genus (p. 213)
ZooBank registration: urn:lsid:zoobank.org:act:084A22C9-D602-4429-891B-8D1E262519B8

Eothenomyina, new subtribe (p. 115)
ZooBank registration: urn:lsid:zoobank.org:act:DAFD1E02-F1C5-49F1-81DA-0546C6CC55D3

Hyperacrina, new subtribe (p. 179)
ZooBank registration: urn:lsid:zoobank.org:act:BFC80816-A71B-4E0B-8E8B-D5D298355D46

Index to the technical names

Each name is entered only once, under the genus in which it is recognized in this book. Names of extant Palaearctic arvicolines printed in bold face are those which are given full status. Family group names are in cmall capitals. Bold face figures refer to the pages of the detailed description.

Voles and Lemmings (Arvicolinae) of the Palaearctic Region

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Abstract As the most species-rich group of Palaearctic rodents, voles and lemmings are frequently used in various research endeavours of fundamental and applied significance. The present work integrates achievements of the genomic era with the traditional taxonomy and provides an authoritative and up-to-date taxonomic guide to the animal group which is of great interest to experts engaged in medical zoology, epidemiology, biostratigraphy, zooarchaeology, evolutionary research, population ecology, animal systematics, biodiversity conservation, museum collection management and many more biological subdisciplines. The text is supplemented by 331 illustrations and over one thousand references. Depicted are morphological details of skull and dentition of each of the 128 species and their distributions are mapped in detail. The book will allow the user to interpret intelligently and cautiously the interrelationships among species of voles and lemmings and to follow the anticipated taxonomic change with a critical eye.

Keywords:
taxonomy, nomenclature, morphology, karyology, molecular systematics, species delimitation, subspecies, zoogeography, distribution modelling

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This is the most comprehensive and up-to-date book dedicated to one of the most important and abundant groups of small mammals.

Professor **Boris Krasnov**
Ben-Gurion University of the Negev

The book represents an extraordinary contribution to current mammological literature and will provide a robust reference platform for further study of the group for a number of decades to come.

Professor **Ivan Horáček**
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